

A pitchy red species, densely clothed (even on the legs and tarsi) with bright golden and ochraceous round scales; the ochraceous scales form on the thorax a patch above each anterior angle and a line on each side of the middle; on the elytra a small spot on the side (about the middle), and a larger oblique subapical patch not reaching the suture; these ochraceous scales also appear golden when viewed obliquely. The scales on the abdomen and pygidium are more silvery. The clypeus has the margins distinctly reflexed and the angles much rounded. Thorax a little narrower than the elytra, one fourth broader than long, distinctly narrowed in front and behind, angular at the sides, regularly convex above. Elytra one fourth longer than broad, moderately depressed above, but not flat; the sides are subparallel, scarcely arcuate, the subapical callosity very little prominent. In some lights the golden scales on the elytra present a mark like an X, embracing the more ochraceous scales.

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Notes touching Recent Researches on the Radiolaria.

By ST. GEORGE MIVART, Zool. Sec. Linn. Soc.

[Read January 17, 1877.]

THE example which has been set by our President in publishing\* from time to time in his successive Addresses a digest and *résumé* of the most recent researches which have been carried on respecting certain of the lowest animal groups, has led me to believe that a similar course might advantageously be taken with respect to the Radiolaria. Our publications already afford, through Dr. Allman's recent labours, the readiest means of obtaining a knowledge of the most modern investigations with respect to various groups of Protozoa; and I have myself found the memoirs referred to most valuable and useful. I hope that other Fellows may adopt a similar course; so that our Journal may become a complete repertory of information respecting all the lower groups of the animal kingdom. No English publication on the Radiolaria exists to my knowledge; and although the most admirable monograph† of Professor Haeckel

\* 'Proceedings' for May 24th, 1875; Journal, vol. xiii. No. 69, p. 261, and No. 71, p. 385.

† 'Die Radiolarien,' 1862.

was, at the time, a complete and exhaustive account, yet, were it even readily and generally accessible, important additions have now been made to our knowledge of these animals since its publication. I venture to think therefore, and my opinion has been confirmed by very high authority (that of our esteemed President), that an account of these beautiful, and in many respects complex, organisms will not be an unwelcome addition to English zoological literature.

Under the name *Radiolaria* are comprised a great number of minute, very varied, and beautiful organisms which are found swimming near the surface of the water, and which considerably resemble the Heliozoa, but are of more complex structure.

Each individual consists of two portions of coloured or colourless *sarcodæ*—one portion nucleated and central, the other portion peripheral and almost always containing certain *yellow cells*. These two portions are separated by a porous membrane called the *capsule*\*; and the whole is invested by a generally very delicate gelatinous layer. The sarcodæ, moreover, sends forth, mostly on all sides, multitudinous radiating, filamentary prolongations of its substance, the *pseudopodia*, which may or may not branch or anastomose.

In most species skeletal structures are developed in the sarcodæ either outside or inside the capsule, or both without and within it, and generally in the form of spheroidal investing networks, or of radiating spines, or of combinations of these, though sometimes reduced to a few filamentary or branched spicula. Whatever its form, the skeleton is almost always siliceous, and is never calcareous †.

The individuals (or zooids) of some species, both of kinds provided with and others destitute of skeletal structures, naturally

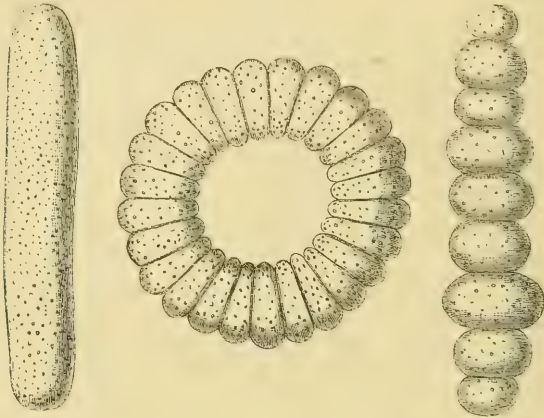
\* Sir C. Wyville Thomson speaks of Radiolarians destitute of a central capsule ('Voyage of the Challenger,' vol. i.). If this is not a clerical error, some very interesting new forms may be expected to be made known by the publication of the 'Challenger's' zoology. But whatever novelties may be forthcoming, forms without a central capsule should, I think, be excluded from the Radiolaria.

† The calcareous bodies found in the extracapsular sarcodæ of *Myxobrachia* I do not regard as forming a real exception. As to the calcareous forms noticed and figured by Sir C. Wyville Thomson ('Voyage of the Challenger,' vol. i. p. 233) under the name of *Calcaromma calcarea*, we must wait for more detailed and exact information. I cannot but think it possible that its calcareous particles may really be extraneous bodies, as also those of *Myxobrachia*.

cohere in compound masses or colonies which may assume various shapes—cylindrical, spheroidal, or like a chain, or even a circlet of beads. There may be many more than a thousand zooids in such aggregations, which may attain a length of 50 millims.

In colonies, the gelatinous investment attains a greater size than in most of the solitary forms.

Fig. 1.



Different forms assumed by colonies of *Collozoum inerme*.  
(After Haeckel.)

The name "Radiolaria" was first used by the great John Müller, who in 1858 united together, under this designation, the three groups known as *Polycystina*, *Thalassicolla*, and *Acanthometra*.

The first Radiolaria noticed were more or less indistinctly referred to in investigations as to the causes of marine luminosity by Tilesius \*, Baird †, and Ehrenberg ‡.

Two definite species, one simple and one compound (*Physematium* and *Sphærozoum*), were distinctly indicated by F. Meyen § as early as 1834.

A great number of fossil kinds were subsequently made known

\* Naturalist to Krüsenert's Circumnavigation in 1803-1806. See Tilesius's 'Ueber das nächtliche Leuchten des Meerwassers,' p. 367, tab. xx a.

† Loudon's 'Magazine of Natural History,' vol. iii. 1830, p. 312, fig. 23 a.

‡ "Das Leuchten des Meeres," Abhandl. der k. Akad. Berlin, 1834, p. 411.

§ Nov. Act. Acad. Leop.-Carol. vol. xvi. Suppl. 1834, pp. 159-164, t. xxviii.

by Ehrenberg, which he assembled together under the name *Polycystina*, and to these living forms were subsequently aggregated.

Professor Huxley, while on board H.M.S. 'Rattlesnake,' discovered certain marine organisms, to which he gave the generic name *Thalassicolla*; and his description in 1851\* first made known the main points in Radiolarian anatomy.

In 1855 John Müller described † certain star-like organisms to which he gave the name *Acanthometra*, and subsequently (as before said) united them with other groups as Radiolaria in a memoir ‡ which is the first great work on the anatomy of both the hard and soft parts of these organisms.

In 1862 Professor Haeckel published his magnificent and classical work 'Die Radiolarien,' containing not only the most complete account of the structure of the whole group, but copious references to all preceding writers, as well as a description of a multitude of new genera and species, with an Atlas of thirty-five beautiful folio plates drawn by himself.

Had this illustrious naturalist done no other scientific work, this alone would suffice to procure him enduring fame.

Since this epoch-making work there have appeared other papers by the same author describing new genera and species, and also papers by Dana, Schneider, Wallich, Stuart, Wagner, Focke, Greef, Archer, Macdonald, Donitz, Cienkowski, Hertwig and Lesser, and Hertwig, which will be enumerated in the list of the literature of the Radiolaria at the end of this memoir, and will be incidentally referred to as occasion requires. It will suffice here to make special mention of Cienkowski's researches § on the reproduction of Radiolarians, and of Dr. Richard Hertwig's admirable paper || on the same subject and on the anatomy of certain forms.

The individual Radiolarians or zooids vary in size from about  $\frac{1}{800}$ " to about  $\frac{1}{20}$ "; but they are for the most part invisible to the naked eye, though rarely, as in *Myxobrachia* (an elongated form), they may attain the length of 14 millims.

Mostly spheroidal, they may yet be conical, cylindrical, lens-

\* Ann. & Mag. Nat. Hist. ser. 2, vol. viii. p. 433.

† Monatsberichte Berlin, 1855, p. 671.

‡ Abhandl. d. könig. Akad. Berlin, 1858, pp. 1-62, pls. i.-ix.

§ Archiv für mikrosk. Anat. vol. vii. p. 371 (1871).

|| 'Zur Histologie der Radiolarien,' 1876.



shaped, or in the form of flattened disks, and such disks may be here and there enlarged by having wide arm-like productions.

The *sarcodē* is a homogeneous protoplasmic substance containing granules. A chitinous membrane divides it, as before said, into an intra- and an extracapsular sarcodē, these parts being directly continuous through minute pores which perforate the membranous capsule. The sarcodē may be extremely fluid, as in *Collosp̄era*, or relatively firm, as in *Acanthometra*.

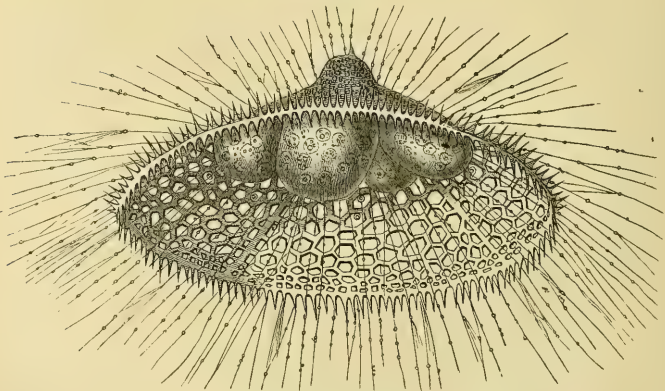
In most solitary forms the capsule is very large relatively to the whole mass, the extracapsular sarcodē being relatively scanty. In some forms, however, the reverse is so much the case that the diameter of the capsule may be but about one fifth of the whole organism, as is the case in *Thalassicolla*. In the compound forms (colonies) the capsules appear as small spheres scattered through the relatively large mass of extracapsular sarcodē and gelatinous investment.

The size of the capsule may vary from about 2 millims. (*Thalassolampe* and *Physematium*) to 0·025 millim. (*Zygostephanus*).

It is formed of a relatively strong membrane perforated by very numerous minute apertures or pores, and sometimes marked by lines dividing its surface into irregular polygonal segments, as in *Thalassicolla*.

Its shape is mostly spheroidal; but this may vary with the shape of the entire organism. It may also be vertically elongated, with terminal or median enlargements, or both; or (as in some

Fig. 2.



*Eucecryphalus Schultzei*, showing the lobed central pseudopodia and capsule and the oil-globules within them. (After Kölliker.)

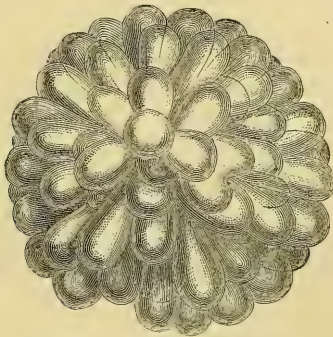
*Cyrtida*) it may have the form of a cone, with its base provided with three or four rounded processes.

In no part of the sarcode do we find habitually contractile spaces (as we do in the Heliozoa); but we may find in the intra- or extracapsular sarcode, or in both, rounded spaces, called *alveoli*, which are mere vacant spaces save for fluid contents, and are devoid of any limiting membrane. They are often considerable both in size and number. The sarcode surrounding some of these alveoli may be so contractile as to occasionally obliterate them, and so, by increasing the specific gravity of the organism, enable it to sink. It is only the more superficially placed alveoli, however, which have been observed so to disappear.

The intracapsular sarcode contains alveoli in *Thalassicolla*, *Thalassolampe*, and *Physematium* only; but, besides certain other formations more or less frequently present, it constantly contains one or both of two sets of structures, which structures, according to the researches of Hertwig, bear to the whole capsule the relation of many simple nuclei or of a single complex nucleus to a cell.

The simple nuclei (the "*wasserhellen Bläschen*" of authors) are rounded homogeneous particles of denser sarcode devoid of investing membrane, and varying in size from about 0.008 millim. to about 0.015 millim., the largest in size being found where the substance is least. They may be so numerous as to fill the capsule, and acquire by reciprocal pressure a polyhedral aspect; or they may be very few and grouped together towards the centre of the capsule; or, finally, when a complex nucleus is present, they may be altogether absent.

Fig. 3.



Nuclear vesicle of *Myxobrachia pluteus*. (After Haeckel.)

The complex nucleus is a small vesicle (the "*Binnenbläschen*" or "*vesicula intima*" of authors) formed of porous membrane similar to, but still more delicate than, the capsule itself. It may be simply spheroidal, or it may be produced on all sides into a number of rounded processes, as in *Thalassicolla*, and still more in *Myxobrachia* (fig. 3). Its contents are mainly clear and homogeneous; but Hertwig has shown that minute bodies become developed within it, which he considers to be nucleoli, and which are said to pass outwards through the membrane and to grow into and become the simple nuclei before described. *Pari passu* with this extrusion of nucleoli and consequent multiplication of nuclei, the *vesicula intima* shrivels. This complex nucleus has as yet only been found in the genera *Thalassicolla*, *Thalassolampe*, *Myxobrachia*, *Physematium*, *Aulacantha*, *Aulosphæra*, *Heliosphæra*, and doubtfully in *Diplosphæra*.

Besides the nuclei, *fatty bodies* (formed of albuminoid substance and adipose matter) are also present in most cases, but are generally absent in young individuals. These fatty bodies have mostly the form of a relatively larger central body with smaller ones scattered round it; and when the capsule is elongated in shape, it has generally one such body near each end.

The intracapsular sarcode may appear colourless and transparent, as in *Heliosphæra*, in many kinds of *Acanthometra*, and others, or it may seem strongly coloured. The commonest colours are yellow, red, or brown; but purple, violet, blue, or olive-green are found in a few species. Two colours rarely co-exist in one capsule. In *Spongocyclia* and *Spongastericus* the inner part of the capsule is scarlet and the outer part golden yellow. The sarcode is not itself coloured, nor does it contain coloured fluids. The pigment exists in granules or small vesicles.

In a very few genera (*Thalassicolla*, *Thalassosphæra*, *Acanthochiasina*, and at least one *Acanthometra*) we find scattered in the sarcode small bodies called "*concretions*," in the form of round or elliptical disks, the sides of which may be flat or more or less strongly convex\*. In *Thalassicolla* these concretions, and also fatty bodies, appear environed by, or connected with, certain peculiar bodies of doubtful nature, to which the name "*Eiweisskugeln*" has been given†. The concretions consist of leucin‡ and tyrosin§, and

\* See Haeckel's 'Radiolarien,' pl. iii. fig. 3.

† Hertwig, 'Histologie,' table iii. fig. 9.

‡  $C_6H_{11}(NH_2)O_2$ .      §  $C_2H_{11}NO_3$ .

are soluble both in acids and alkalies. It may be that they are undigested remnants of food.

Other bodies \*, of a crystalline structure, are found in a very few forms, such as *Collozoum*, *Sphærozoum*, *Thalassicolla*, and *Collosphæra*. Those in the last-named genus are about  $\frac{1}{80}$ ''' long. These crystals are said to be insoluble not only in cold and hot water, but even in cold or hot acids and alkalies.

In a single Radiolarian (*Physematium Müllerii*) Haeckel found scattered round the inside of its capsule groups of three to five pear-shaped cells 0.05-0.06 millim. in length, with their apices mediad †, each enclosed in a membrane and with a granular nucleus. The broad end of each group lies against the inner surface of the capsule. Haeckel suspects that it may be perforated, and so serve as a channel of communication between the intra- and extracapsular sarcode. He calls these groups of cells "*centripetal Zellgruppen*."

As before said, the extracapsular sarcode invests the capsule more or less thickly on all sides, and is itself invested externally by a more or less perceptible gelatinous layer; but no membrane exists beneath or outside that layer.

Alveoli are present in this part of the sarcode of a few simple Radiolaria (*Thalassicolla*, *Aulacantha*) and in all the compound forms, where their great number and size seem the main conditions of the volume of each colony. One excessively large nucleus may occupy the centre of the colony, as in *Collosphæra*, showing one large central alveolus, with circumferential fully-developed capsules and other more central capsules in process of development, also many yellow cells amongst the radiating pseudopodia and the circumferential capsules. The alveoli may, on the contrary, be much larger superficially and smaller within, as in *Thalassicolla*; they are, of course, bounded on all sides by the sarcode, and in the complex forms are bordered by those of the pseudopodia, which radiate inwardly from the several zooids.

The extracapsular sarcode also sometimes contains pigment which is generally black, or black-brown, or red-brown, or dark violet. It is aggregated in granules or vesicles, and is generally collected towards the deepest layer next the capsule.

Nothing at all resembling concretions is found in the external

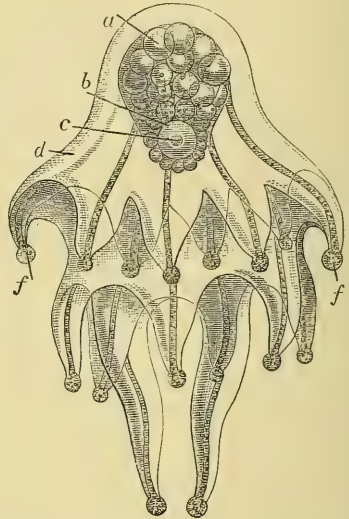
\* See Müller, Abhandl. Berlin, 1858, pl. viii. fig. 9; and Haeckel, *l. c.* pl. iii. fig. 3.

† 'Radiolarien,' pl. iii. fig. 7; and Kolliker's 'Icones Histologicæ,' pl. iv. fig. 7.



sarcode save in the exceptional form *Myxobrachia*. In that genus, however, small calcareous bodies are to be found collected towards the ends of its depending processes. These bodies closely resemble the coccoliths and coccospheres which have been found so extensively at the bottom of the sea. It seems to me not improbable that these bodies are the remains of food; and that the same may be the case with "minute echinated calcareous

Fig. 4.



*Myxobrachia pluteus*. *a*, extracapular alveoli; *b*, capsule; *c*, nuclear vesicle; *d*, gelatinous substance; *f*, coccolith-like concretions at the end of the arm-like processes. (After Haeckel.)

spheres, looking like the rowels of spurs," described as scattered irregularly in the gelatinous outer substance of *Calcaromma calcaria*, a new form noticed and figured by Sir C. Wyville Thomson\*.

Certain peculiar structures already mentioned (the "yellow cells") are very characteristic of the Radiolaria, being found in all except some *Acanthometra* forms, though their number is very inconstant in the same species †. They are nucleated, and their yellow protoplasmic contents, which contains starch-granules, is enclosed in a distinct membrane.

\* 'Voyage of the Challenger,' vol. i. pp. 232-33.

† See representations in Archiv für mikrosk. Anat. vol. vii. pl. 29. figs. 30-36.



Scattered round the capsule, they, in the complex forms, often wander some distance into the circumcapsular gelatinous mass.

Hertwig\* deems it probable that they arise from nuclei which pass out from within the capsule; but there is no evidence for this; and Cienkowski† having found them vigorously multiplying in dead Radiolaria, suspects that they may be parasitic organisms. This latter view is opposed by Hertwig on account of the great constancy of their presence in almost all Radiolaria. But undoubted parasites are present with remarkable constancy in many higher animals, while several difficulties disappear if we may regard them as parasites. It would, first, account for no other satisfactory explanation of their origin having been arrived at; secondly, for their greatly varying number; thirdly, for their survival and increase amidst the decomposition of the individuals in which they live; and, lastly, it would explain the anomaly of their existence in such creatures as Radiolaria—*i. e.*, the anomaly of unicellular animals containing true cells within them. For the yellow cells are undoubted cells multiplying by spontaneous division of their cell-contents, each division surrounding itself by its own cell-wall before the dissolution of the mother cell. Their size varies from about 0.005 millim. to about 0.025 millim.

Certain yet other extracapsular bodies have been noticed by Hertwig‡ in *Collozoum inerme* surrounding the central capsules, but also wandering far from them into the gelatinous investment. They are mostly spheroidal, and from 0.02 millim. to 0.04 millim. in diameter, though they may be more elongated. Each contains small fat-particles, and osmic acid brings also into view some large nuclei. The nature of these bodies is problematical; but it is not impossible that they may be new central capsules in an incipient stage of existence. They may, however, be stages of the reproductive process, in considering which they will be again referred to.

\* 'Histologie,' p. 19.

† Archiv für mikrosk. Anat. 1871, vol. vii. He also tells us that yellow-coloured specks, which might be taken for young yellow cells, were due to the Radiolarian observed having fed on yellow *Tintinnoids*.

‡ *L. c.* p. 37. He considers that Haeckel's "extracapsularen Oelkugeln" (p. 149, pl. xxv. fig. 13) may be the same bodies (though they are less regular in form and more numerous than Haeckel's), as also Müller's "sehr kleine Nester" (Abhandl. Berlin, 1858, p. 5) and Cienkowski's "zusammengedrückte Bläschen" (Archiv f. mikrosk. Anat. vol. vii. 1871, p. 378, pl. xxix. fig. 29), which looked quite like young capsules.

Finally to be noticed amongst the soft parts is that mass of delicate sarcodic prolongations, the pseudopodia. These radiate from the deepest part of the extracapsular mass, passing between the alveoli where these are present, and perforating the gelatinous investing coat. They radiate in all directions; and thus in the compound forms the pseudopodia of all but the superficial zooids, and the inwardly directed pseudopodia of even the superficial ones, pass into the soft mass, between its included alveoli. In those single forms, however, which have a bilateral symmetry, the pseudopodia radiate accordingly, and are commonly longest and most numerous from the long axis of the body. They may even stream forth from the ends only, as in *Diploconus*; and when the skeleton forms a conical shell with special apertures at its base, it is in the latter situation that the pseudopodia are longest.

The pseudopodia, like those of the Heliozoa, have generally much persistency of direction and little flexibility. Nevertheless they may bend much and can be retracted, an action distinctly observed by Hertwig in *Thalassicolla*. In some species granular particles of the sarcode may be plainly discerned slowly streaming to and fro along the pseudopodia.

These processes appear to branch in some species and not in others and similarly they may or they may not anastomose. In some forms they traverse hollow canals enclosed within parts of the skeleton, appearing at the apices of the spines thus perforated.

Their number is generally great, over a thousand in an individual *Thalassicolla*. On the other hand, they may be so few that their number may serve as a distinctive character, as in *Acanthometra*. Their length may more or less exceed the diameter of the body, as in *Ethmosphæra* and others, or scarcely equal to a quarter of that diameter, as in *Trematodiscus* and *Spongoicyclia*.

In a few bilaterally symmetrical genera (*Euchitonia*, *Spongoicyclia*, and *Spongastericus*) there is a *flagellum* attached to the middle of one end of the body. It is formed of homogeneous sarcode, and is much thicker than the pseudopodia, which it may but very little exceed in length, though it may much exceed them. It has the form of a very elongated cone, and is generally bent in a double flexure instead of being straight like the pseudopodia. It appears to move slowly.

In *Acanthometra* and its allies the sarcode, after death, becomes retracted, so as to form blunt prominences corresponding to the

sheaths of sarcode which in life envelop the spines to their apices. At the summit of each such blunt prominence there is a circle of small papillæ, which consist of the remains of the retracted pseudopodia.

As has been said, a system of internal hard parts is more or less developed in almost all Radiolarians. The few yet known utterly devoid of a skeleton are the simple forms *Thalassicolla*, *Thalassolampe*, and *Myxobrachia*\*, and the compound form *Collozoum*. The skeleton consists generally of silex only, and is never calcareous †. In some forms, however, it consists only of a peculiar cartilaginous animal substance “*acanthin*” ‡. In some forms this acanthin becomes, with age, more or less replaced by silica.

The form of the skeleton varies greatly, from extreme simplicity to extreme complexity. It may be described as consisting of two systems of parts:—

- A. A system of circumferential (tangential) parts ;
- B. A system of radiating parts.

Either of these may exist (alone or with the other) in different degrees of development, from the most rudimentary condition up to an extreme degree of complexity.

These parts may also both exist in so fragmentary a state and in such a complex entanglement, as to form a spongy skeletal network which may coexist with simpler parts of either of the two skeletal systems or by itself alone. Thus the spongy network, if it were considered a third kind of skeleton, might be said to pass gradually either into the circumferential or into the radial system of parts.

Both systems of parts may exist, in different groups of Radiolarians, either externally to or more or less within the capsule, or both within and without it simultaneously.

Both the circumferential and the radial parts may be either

\* I do not regard the calcareous formation found in this genus as skeletal.

† Sir C. Wyville Thomson has (as before noted) described shortly and figured a Radiolarian, *Calcaromma calcarea*, in which calcareous spheres like “the spicules of a Holothurian” were found. Until we have more detailed information, I hesitate as to the truly skeletal nature of these calcareous particles. See ‘Voyage of the Challenger,’ vol. i. p. 233, fig. 51.

‡ A substance much like keratin. It is eaten into and destroyed by sulphuric acid.

solid or, more rarely, hollow; and in the latter case they are traversed by the sarcode.

The circumferential system appears, in its most rudimentary condition (in the simple form *Physematium*\* and the compound form *Sphærozoum italicum*†), as short, separate, solid, needle-like, but more or less curved spicula. They are placed tangentially around the capsule. Some of those of *Physematium* exhibit the next degree of complication in that they give off at intervals and at right angles short pointed processes.

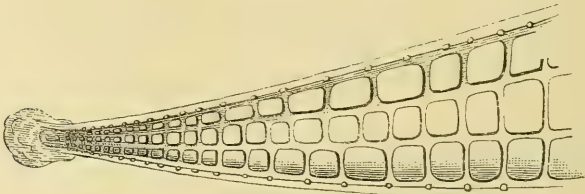
A step further is shown in the exceedingly long and delicate, but hollow spicules of *Aulacantha*‡ and *Thalassoplaneta*§. Those of the former genus are so numerous and relatively minute as to form an investing layer towards the outside of the extracapsular sarcode with its large alveoli. Those of the latter genus are of enormously greater size relatively.

Next comes the compound genus *Rhaphidozoum*, round the capsules of which we find simple spicula, like those of *Sphærozoum italicum*, but with short secondary processes (like the more complex of those before mentioned as occurring in *Physematium*); and, in addition, other spicula, each formed of four such needles radiating from a common point||.

Another step in advance, as regards complexity, is by the compound species *Sphærozoum ovo-di-mare*¶, where each spiculum is in the form of a short rod which subdivides at each end into three radiating processes, and these may be provided with secondary processes, as in *S. punctatum*\*\*.

We have seen that the needle-like spicula of *Aulacantha* are so numerous as to form a disconnected investment and network of

Fig. 5.



*Cornutella scalaris.* (After Ehrenberg.)

\* See 'Radiolarien,' pl. iii. fig. 9.

† *L. c.* pl. ii. fig. 1, and pl. iv. figs. 4 & 5.

|| *L. c.* pl. xxxii. fig. 11.

\*\* *L. c.* pl. xxxiii. fig. 7.

† *L. c.* pl. xxxiii. fig. 2.

§ *L. c.* pl. iii. fig. 13.

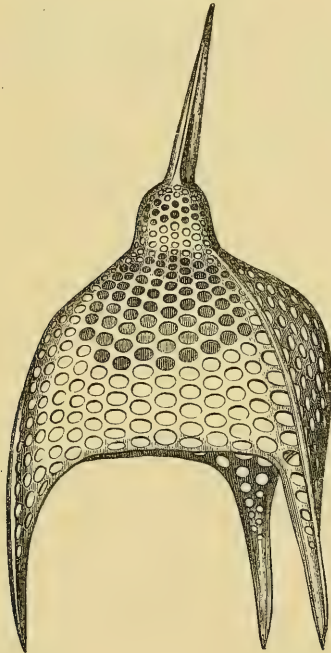
¶ *L. c.* pl. xxxiii. fig. 6.

detached parts. Now if we conceive these to be united together into one complex structure, we may thence derive all the other forms of circumferential Radiolarian skeletons. First, by union in an irregular manner, we obtain a spheroidal investing network with irregular intervals, as in *Cyrtidosphæra* and *Collosphæra*.

Secondly, let these be united with regularity, and we get such a form as *Heliosphæra inermis* \* (the skeleton of which consists of bars enclosing equal-sized and perfectly regular hexagonal spaces); and if the skeletal parts be hollow, we get such a structure as *Aulosphæra elegantissima* †.

Thirdly, let the intervals of the network be greatly reduced in relative size, as sometimes in *Collosphæra* ‡, and the sphere be

Fig. 6.



*Dictyopodium*, sp.? (After Wyv. Thomson.)§

\* *L. c.* pl. ix. fig. 1.      † *L. c.* pl. xi. fig. 6.      ‡ *L. c.* pl. xxxiv. fig. 4.

§ I herewith take the opportunity of acknowledging the kindness of Prof. Sir C. Wyville Thomson and Messrs. McMillan & Co., in allowing me the use of woodcuts fig. 6 and fig. 8 hereafter represented. Both these have already appeared in the 'Voyage of the Challenger.'



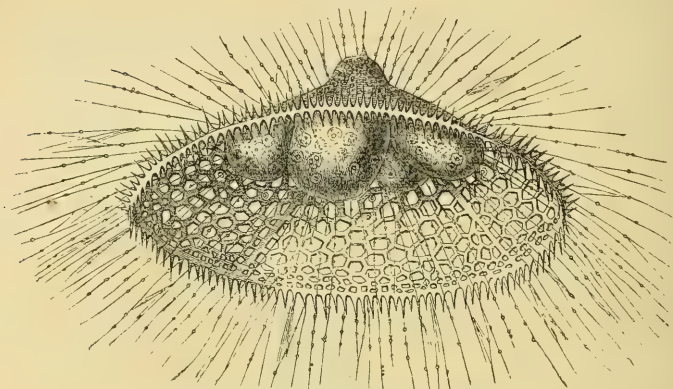
drawn out at opposite poles and be irregularly constricted meridionally and equatorially, and we get such a form as *Botryocampe*, one of a series of Polycystinian forms.

Let this be open at one pole, and we get such forms as *Eucyrtidium*, *Cyrtocalpis obliqua*, and *Cornutella* (fig. 5).

Let the margins of the open end be produced into spines, and we get such forms as *Lychnocanium* and *Dictyopodium* (fig. 6).

Let one pole be greatly expanded and we have *Eucecryphalus*,

Fig. 7.



*Eucecryphalus Schultzei*. (After Kölliker.)

and finally we have *Litharachnium tentorium*, which latter exhibits, in the delicacy of its skeletal bars, a return towards the circumferential network of *Aulacantha*.

Fourthly, let the circumferential skeleton, as it is in *Cyrtidosphæra*, be conceived as having its apertures greatly reduced and its solid parts augmented in massiveness while they are reduced in number, and we get such forms as *Zygostephanus*\*, *Dictyocha*†, and *Acanthodesmia*.

But the circumferential skeleton may not only form a single layer investing the capsule, for there may be two, three, or even six more or less completely developed skeletal spheres concentrically investing the capsule, as in *Arachnosphæra*. These complex concentric structures, however, are intimately connected with and more or less dependent upon radiating skeletal elements, so that they will be best considered along with the radiating structures referred to.

\* *L. c.* plate xii. fig. 2.

† *L. c.* plate xii. figs. 3-6.

All the skeletal parts yet treated of are placed without the capsule ; but a circumferential skeleton may exist within, or simultaneously within and without it.

Thus we may have a spheroidal shell with small perforations as in *Cœlodendrum*\*, and this may be accompanied with one (*Heliodiscus*†) or two (*Actinomma*‡) other concentric shells external to it.

The circumferential skeletons hitherto considered have been more or less nearly spheroidal ; but they may be (as in the *Discida*) so compressed as to form flat, rounded, or elliptical disks, the opposite sides, however, being generally more or less convex, so as to make the whole shell to a greater or less degree lens-shaped. These shells, however, are not merely circumferential, but have a skeletal partition dividing their interior into two by a transverse partition, which extends everywhere to their margins ; and thus they will be better considered when we have entered upon the second or radial system of skeletal parts, to which we may now proceed.

With the second or *radiating system of parts* we have already unavoidably made some acquaintance in considering the circumferential skeleton. Thus in *Botryocampe*, *Eucyrtidium*, *Eucecryphalus*, *Dictyopodium*§, *Dictyocha*, *Zygostephanus*, and *Acanthodermia* we have seen certain centrifugal spines radiating from the surface of the shell.

The pure and simple radial system is, however, to be seen at its simplest in *Plagiacantha*, where the point of union of the radii does not lie within the capsule but eccentrically beside it.

Next may be mentioned the long spines of *Aulacantha*||, which are hollow with numerous barbs towards their apices, and which impinge by their proximal ends against the outside of the capsule. Also the barbed spines of *Aulosphæra elegantissima*¶, which spines radiate from the points of junction of the circumferential hollow bars which form its beautiful and symmetrical investing shell before noticed.

From the outside of a circumferential shell long spines may radiate in all directions, and from such spines fibres may be given off at regular and coinciding intervals, which fibres may, by their junction, form as many as six delicate concentric spheres, succes-

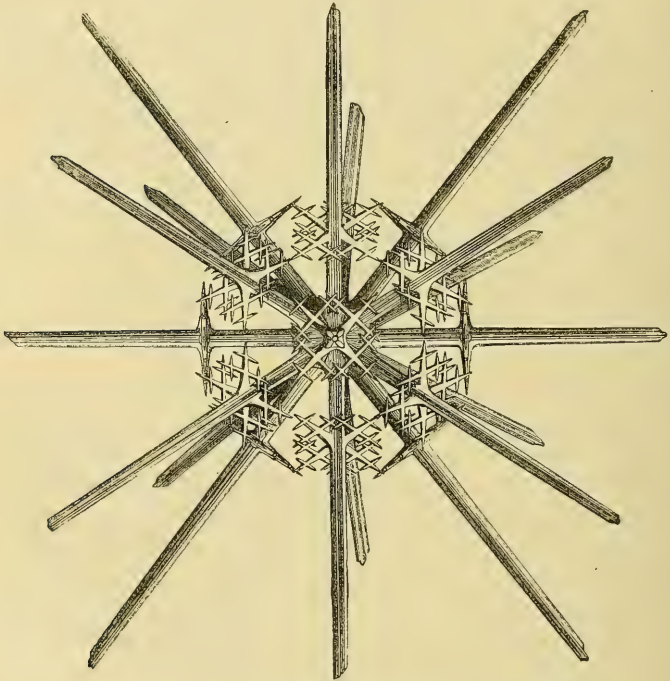
\* *L. c.* pl. xiii. fig. 3.    † *L. c.* pl. xvii. figs. 5-7.    ‡ *L. c.* pl. xxiii. fig. 6.  
§ See *antè*, fig. 6.    || 'Radiolarien,' pl. iv. fig. 2 & 3.    ¶ *L. c.* pl. xi. fig. 5.

sively investing the innermost but extracapsular shell from which such radii start. This condition is seen in *Arachnosphæra myriacantha*, and has been already referred to as occupying circumferential structures depending upon radial parts.

The radial parts hitherto referred to are all extracapsular; but radii may proceed from an intracapsular spheroidal shell, as in *Heliodiscus*\* and *Actinomma*, and also in *Rhaphidococcus*†.

They may so radiate and at the same time assume the most beautiful arborescent structure, which may be solid, as in *Cladococcus*‡, or hollow, as in *Cælodendrum*.

Fig. 8.



*Xiphacantha* obtained during the 'Challenger' Expedition §.  
(After Wyv. Thomson.)

The truly radiating structure *par excellence* is found, however, in *Acanthometra* and the allied genera, where we often find radii only, with no vestige of a circumferential skeleton. The radii

\* *L. c.* pl. xvii. figs. 5-7. † *L. c.* pl. xiii. fig. 5. ‡ *L. c.* pl. xiv. fig. 6.

§ 'Voyage of Challenger,' p. 235, fig. 53.

may or may not be of similar length, but they always meet within the capsule and consist of twenty acanthin spicula.

They may merely meet together centrally, and be all alike, as in *Acanthometra*.

On the other hand, the differences in their length and size may be so great as to make the body conspicuously bipolar, as in *Amphilonche*, where two spicula are greatly in excess of the others.

Four spicula may be in excess, to a less degree, forming two long axes at right angles, as in *Acanthostaurus*\*.

Moreover the processes may give forth transverse processes, as in *Xiphacantha* (fig. 8); and these processes may be very complex, as in *Lithoptera*†.

The spicula may not merely meet together, but they may ankylose together centrally, as in *Astrolithium* and *Staurolithium*.

Two other very exceptional conditions may obtain:—(1) The spicula may merely adjoin when they meet, but instead of regularly radiating on all sides, may all be directed one way, diverging irregularly from one polar axis, as in *Litholophus*‡.

(2) The spicula may be ten in number, and go right through the central capsule in all directions, each spiculum perforating the capsule's wall in two places, the spicula meeting but not in any way uniting centrally.

But radial elements may either join or both join and ankylose, when one or more circumferential shells also exist, the radii perforating them and either simply joining or ankylosing together in the centre, as in *Dorataspis*, *Halliommatidium*, and *Aspidomma*.

One of the most peculiar of all Radiolarian shells is that of *Diploconus*§, where we have two very large polar spicula (as in *Amphilonche*) united with ten short, cylindrical, radiating spicula in the middle of the capsule by absolute ankylosis. To this structure there is added two siliceous homogeneous cones, with their apices coinciding with the central mass and with serrated margins at the open ends, from the middle of each of which protrudes one of the large polar spicula. Each of these cones may be conceived as formed of diverging spicula (like those of *Litholophus*) united together; and thus *Diploconus* would be like *Litholophus*, with a double set of opposite, modified, and fused-together spicula, to which other ankylosed spicula, like those of *Amphilonche*, are added.

\* *L. c.* pl. xix. fig. 5.

† *L. c.* pl. xx. fig. 1.

‡ *L. c.* pl. xix. fig. 6.

§ *L. c.* pl. xx. fig. 7.



We may now consider those Radiolarian skeletons which were before spoken of as more or less flattened or lens-like capsules, each with a median partition. Such median partition may be taken as representing the radial elements of the skeleton, and the outer shell, of course, as the circumferential portion.

As before said, the transverse partition extends everywhere to the united margins of the two external halves of each shell; and thus there comes to be on each side of the median partition a cavity bounded externally by the concave surface of one of the two external plates; these plates are irregularly perforated; while the internal median partition may consist of a number of concentric rings united together at regular intervals by radiating centrifugal bars of similar size to the concentric rings, as in *Trematodiscus*.

These structures may include a spheroidal shell within them, or even three concentric shells of the kind as in *Coccodiscus* \*.

The shell may be like *Trematodiscus*, except that it is produced on three sides into three arm-like prolongations, as is the case in *Euchitonia*; and these arms may be further united by an extension of similarly formed shell between them, which extension increases with age.

The shell may have four very elongated arms, as in *Stephanastrum* †.

Instead of the median partition being formed of a number of concentric rings, it may be so formed that the parts representing such rings may take the form of a continuous spiral band, starting from the outside of a very small centrally placed ring. This is the case in *Stylospira*.

Finally, the maximum condition of complexity, with a special arrangement of parts, is attained in *Lithelius*. To understand this shell, which is spheroidal, or an elliptical spheroid, we must imagine a shell, like that of *Stylospira*, made so convex on each side that the whole is nearly spherical. Simultaneously with this change the central partition must be widened out on each side so as to fill up the hemispherical vacuity which would otherwise exist on each side of it; but the continuation of the centrifugal and circumferential bars must not be imagined to form solid partitions, but to be perforated on each side of each cavity, so as to place all the adjacent chambers in mutual communication. Thus would be produced a set of chambers (all opening into adjacent

\* *L. c.* pl. xxviii. figs. 11 & 12.

† See Ehrenberg, *Abhand. k. Akad.* Berlin, 1875, pl. xxv. fig. 1.



chambers on all sides) winding spirally round an axis placed at right angles to the plane of the original median partition, which we have ideally enlarged.

Another mode of conceiving the structure of this shell is to first conceive a central hollow die with successive series of hollow dice placed, one set outside the preceding, all round it so as to form one whole. Secondly, to imagine these dice to have their surfaces cut in curves so that they may be mutually adjusted, and thus form a sphere of successive concentric layers of hollow dice. Then to imagine each die to have a perforation made in each face (six, of course, to each), the perforations of adjoining dice corresponding in position so as to place their hollow interiors in communication—successive concentric layers of hollow communicating chambers being thus produced. Finally, we must imagine a slight twist to be given to the complex whole, so that instead of concentric layers we may have a spiral arrangement of the chambers and of their perforated separating walls, which would thus have come to wind round a single longitudinal axis.

We come now to that system of confused and confounded radiating and tangential parts which together form the spongy kind of skeleton.

The entire skeleton may consist of this kind of structure exclusively and be discoidal, as in *Spongodiscus* \*, or cylindrical with radiating spines attached, as in *Spongurus* †.

The spongy tissue may include a concentric shell like that of *Trematodiscus*, as is the case in *Spongoeyclia* ‡, or surround two or three concentric shells, as in *Dictyosphagma* § and *Spongodictyum* || (or *Dictyosoma*).

But not only concentric spheres, but also strong radii proceeding from their exterior may coexist with a spongy mass, as in *Spongosphæra* ¶.

Finally, a spongy mass may lie entirely outside the capsule and be connected with two spheroidal intracapsular concentric shells by means of radial spines, as is the case in *Rhizosphæra* \*\*.

Such are the main forms presented by the skeletons of the Radiolaria which are as yet known.

Before leaving this portion of my subject, I may be permitted to remark that to my mind it seems evident that these beautiful,

\* *L. c.* pl. xii. figs. 14 & 15. † *L. c.* pl. xxvii. fig. 1.

‡ *L. c.* pl. xxviii. fig. 2. § *Abh. k. Ak. Berlin*, 1858, pl. ii. figs. 9-11.

|| 'Radiolarien,' pl. xxvi. figs. 4-6.

¶ *L. c.* pl. xxvi. figs. 1-3. \*\* *L. c.* pl. xxv. figs. 1-10.

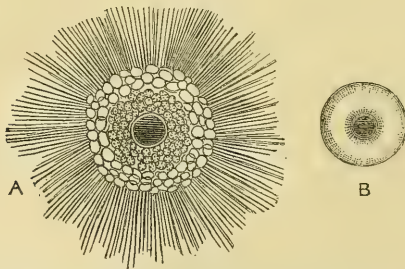
symmetrical, and complex forms cannot be due to the action of *natural selection*, and *sexual selection* can of course take no part in forming such organisms as these. We seem here to have forced upon our notice the action of a kind of organic crystallization, the expression of some as yet unknown law of animal organization, here acting untrammelled by adaptive modifications or by those needs which seem to be so readily responded to by the wonderful plasticity of the animal world.

*Impressionability, Locomotion, and Nutrition.*

The life-processes of the Radiolaria are similar to and are carried on by similar means as those which exist in the *Polythalamia*. Except in the existence of a central capsule and of yellow cells (the nature of which is so doubtful), nothing in the shape of organs is perceptible; and the granules or other matter found within the sarcode can circulate freely throughout its substance. Yet there is some evidence that this structureless sarcode ministers to a certain appreciation of light, since Professor Haeckel found that in a few hours these organisms would cross and recross a glass vessel in order apparently to reach its more illuminated side. Possibly, however, as the Professor himself remarks, this movement may have been really due to currents setting in towards the warmer (which was of course the lighter) side of the vessel.

Radiolarians also seem sensible to heat, since in hot weather they descend to cooler strata of the sea instead of remaining close to the surface, as in weather less warm. They also show, as might

Fig. 9.



*Thalassicolla nucleata*. A. Showing the alveoli expanded and the pseudopodia protruded. B. Contracted. (After Hertwig.)

be expected, sensibility to touch, in so far as they withdraw their pseudopodia and contract their bodies upon the occurrence of any

slight shock, while upon the return of tranquillity they resume their expanded condition; and Hertwig has not only found this to be the case, but also that the external alveoli will close up and disappear with the body's contraction.

Very slight pressure also interrupts the flow of that protoplasmic current and granule circulation which normally exists.

The pseudopodia are never drawn back within the capsule, as is evident by the volume of the capsule remaining constantly the same, though its form may change in some compound Radiolarians.

The animals are very delicate, and are mostly killed by the mere act of catching them in a net. The Polycystine forms are most often taken in a living state; but the Acanthometrine forms are generally dead when captured. In order to keep these animals any time alive, the water in which they are must be kept pure and changed daily and considerable space must be allowed to each animal. Haeckel found the Acanthometrine forms to be the most sensitive and delicate, and these qualities to decrease serially in the following groups:—(1) *Sphærozoida*, (2) *Collosphærida*, (3) *Cladococcida*, (4) *Collida*, (5) *Cyrtida*, (6) *Ethmosphærida*, (7) *Ommatida*, (8) *Spongida*, and (9) *Discida*.

The motions manifested by the Radiolaria are like those shown by the Polythalamia, but weaker, slower, and less obvious. Motion seems to be confined to the extracapsular sarcode, though the capsules of some compound species have been observed to change their shape. The motions are produced by granule streams, as in the Polythalamia. But these do not result in creeping movements as in them, inasmuch as the Radiolaria are essentially floating organisms, and generally have their pseudopodia far extending on all sides. It is a problem how they effect this swimming motion, since their specific gravity is greater than that of water. It is possible they may overcome gravity by active motions of their pseudopodia, or by expanding them distally at the surface of the water so as to act as a sort of float. The contraction and expansion of the alveoli would explain the rising and sinking of such forms as *Thalassicolla*; but, then, most Radiolaria have no alveoli. They can move on solid surfaces by successively contracting their pseudopodia after adhesion, an action which has been observed by Haeckel in his *Collida*, *Cyrtida*, *Ommatida*, and *Discida*. The pseudopodia may ramify, then broaden out at their ends and apply themselves to an object, over which the Radiolarian rolls itself by

successively contracting such applied pseudopodia, just as an *Echinus* rolls itself over by contracting serially its adhering ambulacral suckers. Many Radiolarians also resemble *Echinus* in that they use their spines as levers. Haeckel has observed a *Lithomelissa* (a Polycystine form with spines round the mouth of its shell) thus raise itself so as to apply the mouth of its shell to the floor.

These creatures nourish themselves in the same manner as do the Polythalamia, but with less rapidity and energy. Moreover, in Radiolarians the food does not reach the middle of the body (as it does in Polythalamians), on account of the capsule, which Haeckel never observed to be traversed by any particles of carmine or indigo supplied for experiments.

They live on Algæ, Diatoms, and Infusoria (especially on *Tintinnidæ*), and other small animal and vegetable organisms found near the surface of the sea. Haeckel has observed Infusoria to become paralyzed by the touch of the pseudopodia of *Aulacantha* and *Thalassicolla*, a fact pointing to the existence in undifferentiated sarcode of a power and property which becomes energetic in the thread-cells of Cœlenterata and other less lowly animals. The food is absorbed into any part of the extracapsular sarcode which the skeleton does not hinder it from reaching. They probably also absorb organic matter dissolved in the sea-water. Very minute objects may often be observed coursing centripetally along the pseudopodia, together with the granule-streams. When the prey is relatively large many pseudopodia surround it, draw it in and close over it; and thus food can be assimilated by the pseudopodia themselves when the formation and condition of the shell prevents its penetration more deeply within the matrix.

Haeckel speculates as to the possibly hepatic nature of the yellow cells, considering it to be not unlikely that they may be an incipient form of liver. But, in the first place, these cells may (as has been said) be parasitic; and, secondly, a liver is, as it were, a comparatively late result of tissue-formation, and could hardly exist in the admittedly tissueless Protozoa.

Abundant silica is manifestly somehow obtained by Radiolarians, either from the sea-water itself or from their Diatomaceous food; and there must be a free interchange of nutritious matter through the capsule (even if solid food does not pass through it), as, in so many, part of the siliceous skeleton is intracapsular. If food *does* ever pass through it, then the existence of the concretions within it may be explicable as food-remnants, as before suggested.



*Reproduction and Growth.*

The reproductive processes of the Radiolaria have as yet been completely worked out in no individual form, and even the early stages of it have been observed only in *Acanthometra* and *Thalassicolla* amongst the single forms, and in *Sphærozoum*, *Collosphæra*, and, best of all, in *Collozoum*, amongst the compound forms. What has been hitherto observed, however, in these different genera is of so similar a character that it seems reasonable to anticipate the existence of similar first stages in Radiolarians generally.

The first observation was made by John Müller in 1856\*, who saw inside an *Acanthometra* (apparently within its capsule) a mass of small Monad-like vesicles in motion, which gave off some very delicate filaments "like those of *Acanthometra*."

In 1858, Schneider† saw moving vesicles inside the capsule of a *Thalassicolla*, the vesicles being provided with protruding and retractile processes and also with flagella.

In 1859, Haeckel‡ discovered that the content of the capsule of *Sphærozoum* breaks up into vesicles, which he observed to vibrate, but he did not notice any flagella. He noticed, however, that the several vesicles each contained within it a whetstone-like crystalline body, such as had been previously found amongst the intracapsular sarcode of the same species. On this account and on account of its supposed exclusion from the digestive process, Haeckel suspected the central capsule to be the generative organ, as Müller, for a time, thought the yellow cells might be.

In the same year he found§, in *Acanthometra tetracopa*, five small bodies like young *Acanthometræ*; but as he found no others in hundreds of *Acanthometræ*, and as they were not observed till after the crushing of the capsule, he suspected that they might have been merely adherent to it and not have come from within it.

Young *Acanthometræ* have the spines only imperfectly developed||, sometimes only eight, and scarcely perforating the capsule or even being as yet quite within it.

As to the compound forms, Haeckel believed that their capsules increased not only by fission but also endogenously; and he also believed that individuals separate themselves and lay the foundation of fresh colonies, for he often found single capsules of *Sphærozoum* and *Collozoum*. He never observed the actual fission of any colony, yet such fission seemed indicated by the beaded (appa-

\* Abhand. d. k. Akad. Berlin, 1858, p. 14. † Müller's 'Archiv,' 1858, p. 41. Radiolarien,' p. 141. § *L. c.* p. 144. || *L. c.* pl. xv. fig. 7.



rently incipiently segmented) form of many colonies (fig. 1, p. 138). Multiplication of capsules by fission he believed to be general in the compound kinds, and it seems to take place irregularly in most species. In *Collosphæra*, however, it can only take place in the young shellless condition found in the middle of the colony, since in the developed capsule the shell would hinder subdivision.

Sometimes shells of *Collosphæra* are found in such a condition as to indicate that they were formed while fission was in progress, a shell sometimes appearing like two shells not quite divided off one from another.

Haeckel also found a *Thalassoplaneta* with two capsules within it\*, and doubted whether the circumstance might not be an instance of the beginning of a colony†; but he decided against this view‡, because of:—(1) the absence of alveoli, present in all known compound forms; (2) the presence of extracapsular pigment-heaps (as in *Aulacantha*, *Thalassicolla*, and *Cœlodendrum*); (3) the presence of hollow spines, also present in the three genera last named; and (4) the finding of a single capsule dead.

Most noteworthy is the fact that he saw§ the contents of *Collozoum* capsules break up into internal masses with oil-globules, one in each, or with one large one in the middle of the divided masses. This he considered as endogenous capsule-formation; but (as we shall see) it may have been an incipient stage of spore-formation.

Haeckel also found oil-globules to be sometimes scattered in the extracapsular sarcode, especially in small colonies in January and February.

In 1871, Cienkowski found|| that the contents of the capsules of *Collosphæra* resolved themselves in twenty-four hours into delicate vesicles, which again broke up into little spheroids¶.

In colonies the capsules of which are so filled, the corpuscles collect together, the alveoli disappearing, and the contents of the capsules begin to move and ultimately swim away as zoospores, passing through the holes of the shell, the ripening, however, of the different capsules not being synchronous.

\* *L. c.* pl. iii. fig. 10.

† This circumstance, as well as the separate capsules of *Sphærozoum* and *Collozoum* sometimes found, much reduces the importance of the distinction between the single and compound conditions of Radiolarian life.

‡ *L. c.* p. 262.

§ *L. c.* p. 148.

|| Archiv f. mikrosk. Anat. vol. vii. p. 372 (1871).

¶ Archiv f. mikrosk. Anat. vii. pl. xxix. figs. 5, 6, & 10, and 'Quarterly Journal of Microscopical Science,' (new ser.) vol. xi. pl. xviii. figs. 5, 6, & 8.

Each zoospore is oval, .008 millim. long, and is provided with two long cilia. Each also contains a crystalline rod and a few oil-drops\*. Other zoospores were noticed which were angular and without cilia, apparently immature†. After twenty-four hours all the zoospores died and dissolved away. These zoospores were probably identical with the swarming vesicles found by Haeckel in *Sphærozoum*.

In *Collozoum* Cienkowski found the capsules multiply by division‡, and containing often small crystalline rods as well as oil-globules; but he deemed the occasional presence or absence of these rods as a matter of no importance. He found the contents of each capsule to break up into wedge-shaped or spheroidal masses§, which then divided into small spheroids. As in *Collo-sphæra*, so also here the colonies at this stage lose their alveoli, while their capsules cohere and press together. Illness prevented Cienkowski pursuing the investigation further; but his observations confirmed Haeckel's as to young capsules being naked, having, in fact, no central capsule.

With a view to seeing whether yellow cells would produce themselves spontaneously, he followed Schneider in extruding *Thalassicolla*-capsules from their investing-mass. The capsules so extruded developed themselves only so far as to produce pseudopodia. He found, as before stated, yellow cells freely multiplying themselves in the dead body of a *Collozoum* colony.

Schneider found || that he could keep *Collozoum* five or six days in a cool temperature and by changing the water daily. He also found that upon dividing a colony each part survived and rounded itself off, and that two colonies placed in juxtaposition became fused together in about twelve hours. The soft parts of two adjoined *Thalassicollæ* seemed to fuse together.

Hertwig has published ¶ by far the most complete and detailed account of the Radiolarian reproductive processes; but even he failed to keep the zoospores alive, so that we still remain ignorant of the stages which may intervene between the zoospore larval stage and that which approaches the mature condition.

\* Archiv, *l. c.* figs. 11 & 12, and Quarterly Journal, *l. c.* figs. 9 & 10.

† Archiv, *l. c.* figs. 16 & 17, and Quarterly Journal, *l. c.* figs. 14 & 15.

‡ Archiv, *l. c.* figs. 25-28, and Quarterly Journal, *l. c.* figs. 20-23.

§ Archiv, *l. c.* figs. 20 & 21.

|| Reichert und Du Bois Reymond's Archiv, 1867, p. 509.

¶ 'Zur Histologie der Radiolarien,' Leipzig, 1876.

Hertwig considers the capsule of *Collozoum* to be a multinucleate cell or syncytium, and agrees with Schneider in thinking that it answers to that part of the sarcode of a Foraminifer which lies within the shell. He considers, therefore, that it is not "an organ," and certainly not a "generative organ."

He says that the capsules multiply themselves by division; but he denies that Haeckel was right in considering the multiplication of contained oil-globules to be a sign of the process, as it occurs also in the beginning of zoospore-formation.

He thinks, however, that capsule-division is preceded by multiplication of nuclei, because in a dividing biscuit-shaped capsule he found at each end of it a heap of nuclei equal to the entire mass of nuclei contained in the smallest single capsules. He does not accept Haeckel's inferred process of endogenous cell-formation, but deems the appearances seen by Haeckel to be really due to different progressive steps in one process of zoospore-formation.

New colonies, he tells us, may more or less certainly be formed in three ways:—

- (1) Probably by fission, inferred from the chain-like aspect of some colonies, as before stated.
- (2) Possibly by the separation of small portions—a process the existence of which was suspected by Müller and Haeckel from the finding of single capsules devoid of alveoli.
- (3) Certainly by zoospore-formation.

It appears to take a capsule several weeks to become ripe for zoospore-formation, and there seems to be various individual peculiarities in the process.

Cienkowski noticed in *Collozoum*, as before said, that some capsules contained crystalline rods within them, while other capsules did not contain any such bodies. Harmonizing with this, the specimens of *Collozoum* examined by Hertwig showed two different kinds of zoospore-formation, one with, the other without crystals.

#### *Zoospores with Crystals.*

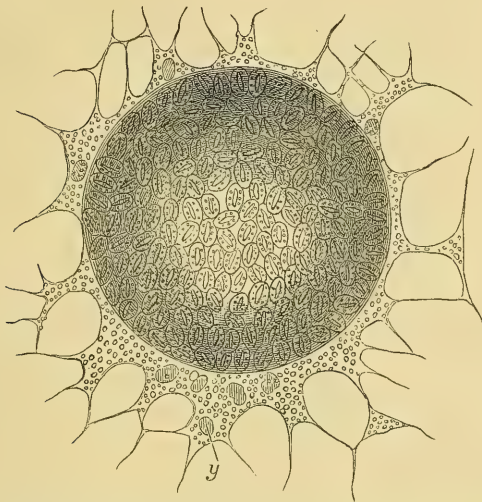
In this kind of reproduction we have in the first stage small capsules containing good-sized nuclei, which subdivide and become heaped together medianly, leaving a space, containing oil-globules, between them and the capsular membrane\*. Then fatty granules and whetstone-like crystals become distinguishable, the crystals

\* Hertwig, pl. i. fig. 1.

having rounded edges and angles with an organic appearance, and being insoluble in both acids and alkalis.

By degrees the crystals, fat-granules, and nuclei become aggregated, so that each capsule is found to contain small bodies, each

Fig. 10.



Contents of a capsule of *Collozoum inerme*, with the bodies above described.  
y, yellow cells. (After Hertwig.)

of which consists of a nucleus with a crystal and some fat-granules. The oil-globules have disappeared, having served to form the fatty granules.

At this stage of development the whole colony sinks, the alveoli dwindle and disappear, and the different capsules become aggregated together towards the middle of the mass. At this stage also a colony will fall asunder with the slightest disturbance, the separated capsules bursting and letting out the contained small bodies, which have already begun to show a tumultuous motion. When discharged, these small bodies are seen to be zoospores, which are at first lively, but which Hertwig found to die in an hour.

Each of the contained bodies or zoospores is oval, with a single flagellum placed at one end, the motion of which is exceedingly lively, so that it might easily be taken for two flagella; and it is possible that Cienkowski may therefore have been mistaken in attributing two flagella to each zoospore of *Collosphæra*. At that end of



the zoospore to which the flagellum is attached its body appears to be homogeneous for about one third of its whole size. The hinder part of the zoospore contains a whetstone-like crystal, so placed as to extend along the axis of the body, and it is surrounded by fatty granules. In the fresh state no nucleus is to be detected; but the application of osmic acid makes manifest a nucleus filling nearly the whole of the homogeneous part of the zoospore.

Unripe capsules contain irregular zoospores which are irregular and angular in shape, and are not yet entirely disconnected from each other, but which nevertheless have often a flagellum.

#### *Zoospores without Crystals.*

The developmental processes which take place without the formation of crystals seem to be more complex and difficult to understand than the others.

The first stage is quite like that of the mode of development with crystals. In the second stage the nuclei become much divided.

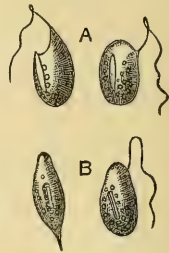
This process goes on while certain of the divided parts cohere together to form masses of different sizes, which together fill the capsule, and consist of nuclei with or without a sarcodic investment.

The oil-globules meanwhile may appear in the form of one large central one\* or may be numerous and equal-sized, or there may be one large central one with smaller ones around it.

The heaps of aggregated nuclei then grew polyhedral, and ultimately each capsule comes to be filled with aggregated masses of larger or of smaller size, and in a more subdivided or a less subdivided condition. As regards the more finely subdivided masses, each such mass consists

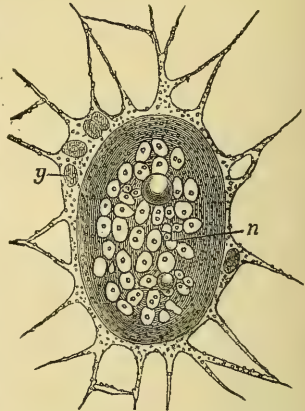
\* In Cienkowski's figure no. 21 we have one oil-globule in the middle of each aggregation, as also apparently in Haeckel's pl. xxxv. fig. 12, and we have a single central one depicted in his plate xxxv. fig. 11.

Fig. 11.



A. Living zoospores of *Collozoum inerme*, with crystals. B. Zoospores of *Collosphera Huxleyi*. (After Hertwig.)

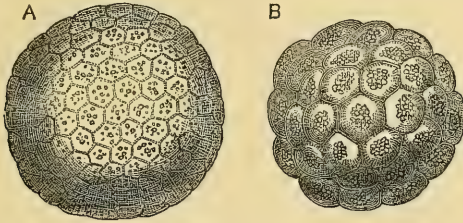
Fig. 12.



Capsule of *Collozoum inerme* without crystals, with oil-globules of different sizes. The nuclei are seen dividing, one (at *n*) into five parts at once. *y*, yellow cells. (After Hertwig.)

of aggregated nuclei only. As regards the less subdivided masses, each such mass consists of nuclei with sarcode aggregated round each nucleus.

Fig. 13.



Heaps of nuclei forming masses with different degrees of subdivision in *Collozoum inerme*. A. Mass consisting of nuclei only. B. Mass consisting of nuclei each with a sarcodic envelope. (After Hertwig.)

The masses which thus exist in two states of subdivision have different destinations, or rather different products, respectively. The oil-globules have now disappeared, but instead fat-granules have appeared in the middle of each nucleus.

At this stage the whole colony sinks and the alveoli disappear, just as is the case at a corresponding stage of the development of those forms of *Collozoum* which are provided with crystals. The next change is for each heap of nuclei to break up, and each part (nucleus, or nucleus and sarcode) becomes a zoospore; but, strange to say, the zoospores are of two kinds, *macrospores* and *microspores*.

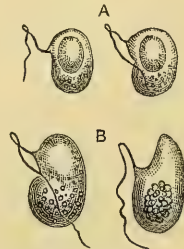
The aggregations above described as consisting of smaller parts (formed of nuclei only) give rise to the microspores; the macrospores are formed from the less divided masses (formed of nuclei with sarcode round each nucleus). The products bear no relation to the size of the aggregations themselves, but to the size of their component parts.

Each zoospore consists of a bean-shaped body, with a long flagellum extending from that end of the body where a nucleus can be made plain by osmic acid. Towards the other end of the body there are fat-granules, but there is no crystal. The macrospores are constantly twice the size of the microspores.

As to the meaning of the difference of spores, Hertwig supposes, naturally enough, that it is related to some difference of function.

As to the difference in manner of reproduction with respect to the presence or ab-

Fig. 14.



A. Two microspores and B. Two macrospores of *Collozoum inerme*. (After Hertwig.)

sence of crystals, Hertwig always found in *Collozoum* one mode of reproduction only in one colony; and he speculates as to whether there may not be two distinct species which are externally very similar. In support of such specific distinctness, he notices that the forms which are provided with crystals have rounded capsules, while those without crystals have elongated capsules—differences before noticed by Müller. Hertwig concludes from all this that the capsule can be no true generative organ. The nuclei act like true physiological nuclei and attract sarcode around them. The swarming is comparable to a very accelerated cell-division, and he compares it with the free-cell formation of botanists.

In *Colloosphæra* and *Sphærozoa*, reproduction takes place, as in the *Collozoa*, with crystals, and each zoospore has a single flagellum.

*Thalassicolla* breeds by the contents of the capsule dividing and subdividing according as the nuclei contained within it are few or many.

When describing the extracapsular sarcode, certain bodies were referred to as “extracapsular bodies,” found by Hertwig in *Collozoum*, and considered by him as perhaps identical with Hæckel’s “extracapsulare Oelkugeln”\*, and Cienkowski’s “zusammengedrängte Bläschen” †, in the same species, and as being, more certainly, the same as the “sehr kleine Nester” found by Müller in *Sphærozoum*.

These structures were described by Hertwig ‡ as being peculiar homogeneous bodies, sometimes surrounding the central capsule so as to cover it, but movable and occasionally wandering, through the extracapsular sarcode, from one capsule to another. Of various, often irregular, shapes, and of various sizes, they seem, when fresh, to contain a heap of small fat-spheres; but nuclei become visible when they are acted on by chromic or acetic acid. They never possess any external, limiting membrane, and their contents seem similar to the contents of an ordinary capsule of *Collozoum*.

Hertwig denies, however, that a great resemblance exists between these bodies and the bodies of aggregated nuclei, already described as found within the capsules of *Collozoum* without crystals, the difference being only in shape, and possibly occasioned by the change from an enclosed to a free condition. He is therefore disposed to regard them as such reproductive masses which have escaped from their capsule before breaking up into zoospores,

\* ‘Radiolarien,’ p. 149, pl. xxxv. fig. 13.

† Arch. f. mikrosk. Anat. vol. vii. 1871, p. 378, pl. xxix. fig. 29.

‡ Abhandl. k. Akad. Berlin, 1858, p. 5.

and to regard their irregular shape as due to incipient divisions, preliminary to such break up.

Thus, as to the whole process, it appears that

(1) With regard to the colonies as wholes, they may perhaps increase by spontaneous fission, or by giving off a single or a few capsules. The existence of these modes of increase has not, however, been actually observed, though it is certain that single capsules (however derived, whether from spores or from segmentation) do exist separately. The colonies may also be increased by juxtaposition, and the mass of an existing colony by the rapid fission of its component capsules, the process taking place centrifugally in the shelled and irregularly in the shellless forms.

It is possible that new young capsules may range themselves round old ones, so producing the above-described "extracapsular bodies," which may, on the other hand, be a stage of spore-formation.

(2) With regard to the capsules themselves, it is certain that they may increase by spontaneous fission into two, three, or more secondary capsules, and that this process may repeat itself indefinitely.

(3) With regard to reproduction by spores, it is certain that such a process occurs in *Acanthometra*, *Thalassicolla*, *Sphærozoum*, *Collosphæra*, and *Collozoum*, and most probably in all Radiolarians.

The spores are formed by the breaking up of the contents of the central capsule into small particles, which become directly transformed into the spores, each spore containing a nucleus and fat-granules, and also a crystalline body when such bodies are found within the capsules in which such spores arise.

Each spore is provided, moreover, with a flagellum, and it is doubtful whether more than one flagellum ever exists to one spore.

The spores may be formed either by the breaking-up of the contents of the capsule directly into them, or by its breaking up into variously shaped masses of various sizes, which again break up into such secondarily formed zoospores. In the latter case (as far as yet observed) the primary cleavage results in the division of the capsule-contents into two sets of masses, the masses of one set being more subdivided than the masses of the other set, which parts respectively give rise to two kinds of spores, microspores and macrospores—bodies having, no doubt, different but as yet unknown functions.

It has been thought, as we have seen, that the same species may have colonies of two kinds—one kind of colony breaking up into spores of two kinds (both without crystals); the other kind of



colony breaking up into spores of one kind only, those with crystals. It is, however, possible that these two processes may indicate two different species which resemble each other greatly, save as to this reproductive process.

Beyond the above described stages, no observations have as yet gone, so that the mode of transition from the zoospore to the capsule stage remains unknown. However, the zoospores have no enveloping membrane, and the young central capsules are in like case. If the latter (capsules) proceed directly from the former, the *Radiolaria* so far resemble the *Heliozoa*; and if the processes observed by Müller as existing in the young enclosed *Acanthometræ* resembled the processes of such organisms as *Actinosphærium*, we have yet another approximation between these two groups of Protozoa.

#### *Modes of Growth.*

As to the modes of growth of the *Radiolaria*, Müller pointed out its three main modes:—(1) the unipolar, (2) the bilateral, (3) the multipolar.

The capsule does not change its shape, but when formed is at once spheroidal, conical, or what not, with or without processes or subdivisions. Thenceforth it only increases in volume.

As to the skeleton, in addition to the three modes of growth above noticed, there must be added that sudden mode of formation, that rapid deposition which seems to take place in the shell of *Collosphæra* (as evidenced by its deposition round capsules in the act of fission) and in the single or in the innermost spheroidal shells of such forms as *Ethmosphæra*, *Cyrtidosphæra*, *Heliosphæra*, *Siphonosphæra*, *Diplosphæra*, *Arachnosphæra*, *Rhaphidococcus*, *Cladococcus*, *Cælodendrum*, *Haliomma*, *Heliodiscus*, *Tetrapyle*, *Actinomma*, *Didymocyrtis*, *Rhizosphæra*, *Spongosphæra*, *Dictyoplegma*, *Spongodictyum*.

Increase, even in the thickness of the network of the shell when once formed, does not seem to take place; for Haeckel found the bars of *Heliosphæra inermis*, *H. tenuissima*, and *H. actinota* constantly the same in size in different individuals of the same species.

*Multipolar growth* takes place in the *Acanthometrine* forms *Sphærozoum*, *Stylodicta*, *Lithelius*, *Actinomma*, &c., and also in the species of spine-bearing *Polycystine* forms and in the twigs of *Cladococcus*. In these the skeletal parts go on increasing at their apices, or (as in *Sphærozoum* and most *Acanthometrine* forms) all round also.

Fig. 15.

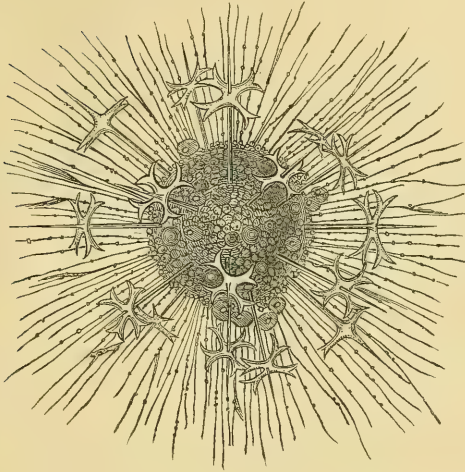


Fig. 16.



*Dorataspis polyancistra*. Fig. 15. Young. Fig. 16. Mature. (After Haeckel.)

Multipolar growth is also exemplified in such forms as *Dorataspis*, *Haliommatidium*, *Rhizosphæra*, *Diplosphæra*, and *Actinosphæra*. Such shells arise by extension of the skeleton from the radii outwards at right angles, and at similar distances from the centre of the shell, the lateral extensions from such radii meeting to form a sphere by their junctions. In the same way, by the development from each radius of successively diverging structures at similar distances are built up many of the successive concentric spheres before described, *i. e.* of those which coexist with radii.

In *Cœlodendrum* alone of all Radiolaria is constant absorption and redeposition known to take place. It must do so here, as the radiating tubules have always thin walls.

Unipolar growth is exemplified in the Polycystine forms, in which at first the shell is a mere cap placed on the apex of the capsule, and thence growing forth on all sides—in the same way the chambers of such more complex Polycystine forms as *Eucyrtidium*, and probably also those with closed bases like *Botryocampe*, though such have not, so far as I know, yet been discovered in process of formation.

The *bilateral* mode of growth is exemplified by *Haliodiscus*\*, in which the outer shell arises as two shields, one on each side of the central shell, each enlarging at its circumference till the two meet.

The *Discida* are formed by a process which may be considered a combination of the bilateral and the multipolar modes. Their median partition is formed by radii which, by the processes they give off at right angles, form the series of concentric or spirally arranged chambers which exist in the median partition and between it and the two outer shields. The two outer perforated plates or shields are formed in the same way as are the bilateral plates of *Haliodiscus*, being, however, nearly quite parallel instead of being much curved as in the last-named genus.

The shells with a spongy skeleton are formed in one or other of the before mentioned ways—in *Spongurus* certainly in the multipolar way.

#### *Distribution of the Radiolaria.*

The *Radiolaria* have as yet been found in salt water only, but there very abundantly close to the surface of the sea and at a little depth beneath the surface, whence they descend in cool or cloudy weather. Until quite recently there was no evidence that they

\* Müller, Abhand. d. k. Akad. Berlin, 1858, pl. ii. figs. 5 & 6.

also inhabit the deeper parts of the ocean. Haeckel, when off the coast of Sicily, found them disappear from the surface after much disturbance of the water by wind, after prolonged rain (though they do not seem much disturbed by a small quantity of it), or after many days of the sirocco. They seem to be particularly intolerant of dirty water, and delight in a smooth sea and pure transparent water at a moderately warm temperature. The voyage of the 'Challenger,' however, has convinced Sir C. Wyville Thomson\* that though Foraminifera are apparently confined to a comparatively superficial stratum the Radiolarians exist at all depths; and he tells us, "in the deposit at the bottom, species occur which have been detected neither on the surface nor at 1000 fathoms, the greatest depth at which the tow-net has been systematically used; and specimens taken from near the bottom of species which occur on or near the surface give us the impression of being generally larger and better developed."

As to their geographical distribution, the same author tells us †, "Radiolarians were met with throughout the whole of the Atlantic, and often in great abundance, the sea being not unfrequently slightly discoloured by them. The forms which appeared in such numbers were usually species of the *Acanthometridæ*, but *Polycystina* and the compound genera were also numerous. The remains of Radiolarians were found in all deep-sea deposits, usually in very direct proportion to the numbers occurring on the surface and in intermediate water. It was frequently observed, however, that when, in deep water, certain species swarmed on the surface, very few of their skeletons could be detected at the bottom. This applies especially to *Acanthometridæ*, and is probably owing to the extreme tenuity of the siliceous wall of their radiating spicules, which may admit of their being dissolved while sinking to a great depth; or probably the spicules may never become thoroughly silicified, but may retain permanently more or less the condition of acanthin. The *Polycystina* seem much less destructible, and occur in abundance on the bottom at the greatest depths. Although the Radiolaria are universally distributed, like the Diatoms, but in a less marked degree, they seem to be most numerous when the specific gravity of the water is low; they specially swarm in the warm and comparatively still region of the south-western Pacific and among the islands of the Malay archi-

\* 'Voyage of the Challenger,' 1877, vol. i. p. 236.

† *L. c.* vol. ii. p. 340.



pelago, where they are much more abundant than in any part of the Atlantic.”

As to the geographical distribution of different species, little can as yet be said, though doubtless when the detailed information collected by the naturalists of the ‘Challenger’ is published we shall then derive much information on the subject. Some species have certainly a very wide range. This is the case, *e. g.*, with *Thalassicolla* and *Sphærozoum*, which have been found both in tropical and extratropical seas.

I should suspect that the exceptionally clear water of the Red Sea, devoid of impurity by reason of its riverless coasts, would be a very favourable station for these animals, unless the heat should be too great. But few forms have yet been seen in the North Sea, yet they exist in Baffin’s Sea and Davis Straits.

As to the Mediterranean, Müller found Acanthometrine forms to predominate at Cette, and Polycystine forms at Nice, together with *Thalassicolla*. At St. Tropez he found all three. The distribution of the shells described by Ehrenberg is very extensive, reaching from the North Atlantic to the South-Polar Sea.

Their *geological* distribution is confined, for the most part, to the Tertiary rocks. If, however, *Traquairia* should be a Radiolarian, they would then extend back to the Carboniferous period. As to the intervening Secondary epoch, the flints of the Chalk are suspected to be partly formed by a redeposition of silica from their dissolved skeletons. Against this, however, Hæckel objects, because of their conspicuous absence amidst preserved Diatoms (so much smaller) and Polythalamian shells (so much more friable). Zittel, however, has shown that they exist in the Chalk, and there are imperfect remains even in the Trias.

Radiolarians, as is well known, largely contribute to form masses of Tertiary rock at Oran and in Barbadoes. They are also found fossil in Sicily, at Ægina in Greece, at Richmond and Petersburg in Virginia, at Piscatavey in Maryland, in Bermuda, between Chile and Bolivia, near Kasan, and in the Nicobar Islands. Only in the last-mentioned locality and in Barbadoes have they been found in large quantities and in many species (100 species in the former locality and 282 in the latter) forming great masses, which attain the height of 1100 feet in Barbadoes, and 2000 feet at Nicobar.

As far as yet known, the most ancient forms appear to be Polycystine Radiolarians—Cyrtydians, especially the *Zygocyrtyda*,—as many as 229 kinds out of the 282 found in Barbadoes being Cyr-

tidans. It must be borne in mind, however, that the skeletons of such forms are amongst those most likely to be preserved.

#### *Classification.*

The best classification yet offered is that proposed by Haeckel, which is as follows\*. He divides the whole group of Radiolarians into two sections:—A. MONOZOA or MONOCYTTARIA, the simple forms, and B. POLYZOA or POLYCYTTARIA, the compound forms.

His Monocyttaria are subdivided into two sections:—A, a. ECTOLITHIA, with the skeleton external to the capsule; and A, b. ENTOLITHIA, with more or less of the skeleton within the capsule. The Ectolithia are further subdivided into (1) the *Collida* (with a skeleton of scattered spicula or none), (2) *Acanthodesmida* †, (3) *Cyrtida*, (4) *Ethmosphærida*, and (5) *Aulosphærida*. His Entolithia he subdivides into (6) *Cœlodendrida*, (7) *Cladococcida*, (8) *Acanthometrida*, (9) *Diploconida*, (10) *Ommatida*, (11) *Spongurida* (with a skeleton wholly or in part spongy), (12) *Discida*, (13) *Lithelida*. His Polycyttaria he divides into (14) *Sphærozoida* (skeleton absent or in the form of scattered spicula), and (15) *Colloosphærida* (skeleton a perforated shell, surrounding the capsule).

I think it would be very convenient, and therefore desirable, to endeavour if possible to unite together these fifteen different groups into large aggregations. Moreover, since Professor Haeckel's admirable monograph appeared, some new forms, the curious form *Myxobrachia* amongst others, have been discovered. Hertwig has also strongly insisted upon the greater importance of the nuclear vesicle (the *vesicula intima*) as a classificatory character than any characters which can be derived from the skeleton. The aggregation or non-aggregation of zooids into colonies seems to me a comparatively unimportant distinction, especially as individual zooids of the compound species are found (however derived) also in a single and separate condition. I cannot therefore but think the division of Radiolarians into two primary groups, the one single, the other compound, as an unnatural separation. As to the possession or non-possession of a nuclear vesicle (Binnenbläschen or *vesicula intima*), I quite agree with Hertwig that it would form a most important distinction; and I should propose to adopt it provisionally, fully bearing in mind that it may be found hereafter to be very widely, if not all but

\* 'Radiolarien,' p. 237.

† The groups of which no characters are here given are characterized later, having been adopted by me from Prof. Haeckel.

universally, present in the group. Anyhow, I would make its presence or absence a primary character, and therefore follow Hertwig in separating off from Haeckel's *Collida* those forms which have the nuclear vesicle, and uniting them with the other genera which possess that structure into a group of VESICULATA. His remaining *Collida* (namely, *Thalassosphæra* and *Thalassoplaneta*) I would associate along with Haeckel's Polycyttaria into a group under the name COLLOZOA.

His *Acanthodesmida*, *Cyrtida*, and *Ethmosphærida* may then be, I venture to think, associated together as ectolithic, non-vesiculate, simple forms, the skeleton of which consists of more than detached spicula; and to this group the old name of POLYCYSTINA may well be applied.

A very important and natural character seems to me to be the possession of a large flagellum; and I would therefore propose to unite in a group of FLAGELLIFERA the genera *Spongocyclia*\*, *Spongodiscus*, and *Euchitonia*.

The meeting together of radii in the centre of the capsule seems to me a very special and peculiar condition; and I therefore regard as unnatural the separation from the thus characterized ACANTHOMETRIDA of forms (Haeckel's *Dorataspida* †) which differ only in having tangential outgrowths from their radii so disposed as by their mutual junction to form an external shell. I would therefore restore to the *Acanthometrida* those of Haeckel's *Ommatida* the radii of which thus centrally meet, as a separate subsection, to which I would restore the old name *Cataphracta*, to distinguish them from the more Acanthometrine forms, or *Typica*.

Again, *Diploconus*, as presenting the special character of centrally-joined radii, I would unite as a third section of the same great group, regarding its conical structure as a mere special modification of radial structure.

The remainder of Haeckel's *Ommatida* I would propose to unite with his *Cœlodendrîda* and *Cladococcida*, as forms possessing an intracapsular more or less spheroidal shell. Moreover I cannot regard the possession of a spongy skeleton as a natural

\* Though Haeckel failed to find this curious organ in two species of *Spongocyclia* (namely, in *S. cycloides* and *S. elliptica*), yet, as it is present in all the seven species of *Euchitonia*, I cannot but think its absence may have been due to some accident, or, at least, that such absence cannot be a character of those two species at all times. If, however, it should turn out to be constantly absent in them, then I think those two species should be eliminated from the group.

† *L. c.* p. 239.

character, existing, as it does, in such different forms as *Spongocyclia*, *Dictyoplegma*, and *Spongurus*. Therefore Haeckel's *Spongurida* seems to me an unnatural group. Accordingly I would remove from that assemblage *Dictyoplegma*, *Spongodictyum*, *Rhizosphæra*, and *Spongosphæra*; and associate them with the above *Ommatida* as ENTOSPHERIDA, dividing the group into four sections—(1) *Ommatida*, (2) *Spongosphærida*, (3) *Cladococcida*, and (4) *Cœlodendrida*.

At the same time I fully recognize that the mode of growth (by absorption and redeposition) of the last-named form is exceedingly noteworthy; and I should be inclined, on that account, to make a distinct primary group of it, but that I suspect an analogous mode of growth may exist, as yet undiscovered, in some other forms.

To Haeckel's *Spongodiscida* I would add the genus *Stylospongia*, as one of discoidal or cylindrical Radiolaria with spongy skeleton with or without radii; and I would unite these (as a subordinate group) with Haeckel's very natural section DISCIDA. As I have said, I cannot think the spongy nature of the skeleton to be an important character for the reasons already mentioned; while if such a form as *Spongodiscus* is to be associated with any other primary group, I think it must be with the *Discida*. I think so, because in them the skeleton is made up of a multitude both of circumferential and radial parts, and the skeleton of *Spongodiscus* is also made up of a multitude of circumferential and radial parts, only these are quite irregularly arranged instead of being regularly aggregated as in the typical *Discida*. To the *Discida* I would further add the genus *Lithelius*: not that I do not attach importance to the peculiarity of the structure of the latter; but I think that if we may add *Coccodiscus* (with its concentric spheroidal shells) to the *Discida*, on the one hand, we may also take into it *Lithelius* on the other.

In this way we shall succeed in reducing the primary groups from fifteen to seven, which may stand as follows:—

1. *Discida*; 2. *Flagellifera*; 3. *Entosphærida*; 4. *Acanthome-trida*; 5. *Polycystina*; 6. *Collozoa*; and 7. *Vesiculata*.

#### Section I. DISCIDA.

Radiolaria mostly discoidal, sometimes elliptical, rarely cylindrical or spheroidal; skeleton in part intracapsular, and consisting always of both circumferential and radial parts, which may be



quite irregularly disposed, but which generally form an external perforated shell with an internal partition or spheroidal mass forming a series of mutually communicating chambers, which are either concentrically or spirally arranged: no flagellum; growth multipolar or centrifugal; no nuclear vesicle.

#### Subsection 1. COCCODISCIDA.

One or more concentric shells included within the internal shell. Genera: *Coccodiscus*, *Lithocyelia*, *Stylocyelia*, *Astromma*, *Hymeniastrum*.

#### Subsection 2. TREMATODISCIDA.

Central chamber not different from the other and concentric chambers. Genera: *Trematodiscus*, *Perichlamydidium*, *Stylodictya*, *Rhopalastrum*, *Stephanastrum*, *Histiastrum*.

#### Subsection 3. DISCOSPIRIDA.

Central chamber not different from the other and spirally arranged chambers. Genera: *Discospira*, *Stylospira*, *Stylospongia*.

#### Subsection 4. LITHELIDA.

Skeleton spheroidal, with the interior containing a mass of spirally arranged chambers. *Lithelius*.

#### Subsection 5. SPONGIDA.

Skeleton with its chambers not separated off, the radial and circumferential elements being irregularly scattered, except that there are often radiating spines. Genera: *Spongodiscus*, *Spongotrochus*, *Spongurus*.

### Section II. FLAGELLIFERA.

Radiolaria with a flagellum. No nuclear vesicle. Genera: *Spongocyelia*, *Spongoastericus*, *Euchitonia*.

### Section III. ENTOSPHÆRIDA.

Radiolaria with an intracapsular spheroidal shell; not traversed by radii. No nuclear vesicle.

#### Subsection 1. OMMATIDA.

Two or three, or more, concentric spheroidal shells. No spongy skeleton.

Subdivision i. *Haliommatida*.

Two shells only. Genera: *Aspidomma*, *Haliomma*, *Tetrapyle*, *Heliodiscus*, *Ommatospyris*, *Ommatocampe*.

Subdivision ii. *Actinommatida*.

Three or more shells. Genera: *Actinomma*, *Didymocyrtis*, *Cromyomma*, *Chilomma*.

## Subsection 2. SPONGOSPHERIDA.

One or more concentric shells, with spongy skeleton annexed.

Subdivision i. *Cladococcida*.

Shell with solid radiant spicula. Genera: *Rhaphidococcus*, *Cladococcus*.

Subdivision ii. *Cælodendrida*.

Shell with hollow radiant spicula. Genus *Cælodendrum*.

## Section IV. ACANTHOMETRIDA.

Radiolaria with radial skeleton the radii of which meet in the centre of the capsule, and consisting more or less of acanthin. No nuclear vesicle; yellow cells generally absent.

## Subsection 1. TYPICA.

Radii devoid of processes diverging from them at right angles, which by their union form a circumferential structure.

Subdivision i. *Acanthostaurida*.

Radii symmetrical, but only meeting at their apices within the capsule. Genera: *Acanthometra*, *Xiphacantha*, *Amphilonche*, *Acanthostaurus*, *Lithoptera*.

Subdivision ii. *Astrolithida*.

Radii symmetrical, but actually united at their apices. Genera: *Astrolithium*, *Stauroolithium*.

Subdivision iii. *Litholophida*.

Radii unsymmetrical. Genera: *Litholophus*, *Actinellius*.

Subdivision iv. *Acanthochiasmida*.

Radii each perforating the capsule twice and adjoining, but not by their apices within the capsule. Genus *Acanthochiasma*.

## Subsection 2. DIPLOCONIDA.

Skeleton a double one, with radii also. Genus *Diploconus*.

## Subsection 3. CATAPHRACTA.

*Acanthometrida* with outgrowths at right angles from their radii forming a circumferential structure. Genera: *Dorataspis*, *Haliommatidium*.

## Section V. POLYCYSTINA.

Simple, ectolithic Radiolarians with more or less compact skeletons, often with unipolar growth. No nuclear vesicle.

## Subsection 1. CYRTIDA.

Shell an external, more or less continuous, but perforated case variously formed, mostly with an open mouth at one pole; shell growing from one pole. No radial skeleton except external spines.

Subdivision i. *Monocyrtida*.

Shell single, without divisions. Genera: *Litharachnium*, *Cornutella*, *Cyrtocalpis*, *Pylosphæra*, *Spirillina*, *Haliphormis*, *Halicalyptra*, *Carpocanium*.

Subdivision ii. *Zygocyrtida*.

Shell divided by a vertical constriction. Genera: *Dictyospyris*, *Ceratospyris*, *Cladospgris*, *Petalospyris*.

Subdivision iii. *Dicyrtida*.

Shell divided by a transverse constriction. Genera: *Dictyocephalus*, *Lophophæna*, *Clathrocanium*, *Lamprodiscus*, *Lithopera*, *Lithomelissa*, *Arachnocorys*, *Dictyophimus*, *Eucecryphalus*, *Anthocyrtis*, *Lychnocanium*.

Subdivision iv. *Stichocyrtida*.

Shell divided by two or more transverse constrictions. Genera: *Eucyrtidium*, *Lithocampe*, *Thyrsoyrtis*, *Lithocorythium*, *Pterocanium*, *Dictyoceras*, *Lithornithium*, *Rhopalocanium*, *Pterocodon*, *Podocyrtis*, *Dictyopodium*.

Subdivision v. *Polycyrtida*.

Shell divided by several transverse or vertical constrictions. Genera: *Spyridobotrys*, *Botryocampe*, *Lithobotrys*, *Botryocyrtis*.

## Subsection 2. ETHMOSPHERIDA.

One, or two or three circumferential shells united by radii ; if one, then formed of a delicate network with irregular meshes. Genera : *Cyrtidosphæra*, *Ethmosphæra*, *Arachnosphæra*.

## Subsection 3. ACANTHODESMIDA.

Shell consisting of a few irregularly united bands. Genera : *Lithocircus*, *Zygotephanus*, *Acanthodesmia*, *Plagiacantha*, *Prismatium*, *Dictyocha*.

## Section VI. COLLOZOA.

Simple or compound Radiolaria ; if single, then with the skeleton in the form of circumferential detached spicula only. No nuclear vesicle.

## Subsection 1. POLYCOLLIDA.

Compound Radiolarians.

Subdivision i. *Sphærozoida*.

Skeleton absent, or consisting only of scattered spicula. Genera : *Collozoum*, *Sphærozoum*, *Rhaphidozoum*.

Subdivision ii. *Collosphærida*.

Skeleton a spheroidal perforated shell. Genera : *Siphonosphæra*, *Collosphæra*.

## Section VII. VESICULATA.

Radiolaria with a nuclear vesicle.

## Subsection 1. COLLIDA.

Skeleton wanting, or consisting only of scattered circumferential spicula. Genera : *Thalassicolla*, *Thalassolampe*, *Aulacantha*, *Physematium*.

## Subsection 2. SPHÆROIDEA.

Vesiculata with one or more concentric extracapsular shells bound together by radii. Genera : *Heliosphæra*, *Diplosphæra*?

## Subsection 3. AULOSPHERIDA.

Vesiculata with a complex circumferential skeleton of hollow bars. Genus *Aulosphæra*.

## Subsection 4. BRACHIATA.

Vesiculata with the extracapsular sarcode prolonged into one or more arm-like processes. Genus *Myxobrachia*.



*The Relations of the Radiolaria to other Organisms.*

That the Radiolaria form a very well-defined and distinct group of Protozoa is admitted on all hands; but the question at present disputed is whether or not the resemblance between them and the Heliozoa is such as to make it desirable to unite them as two subdivisions of one larger group, itself distinct from all the other larger groups of Protozoa. In his latest paper on the histology of the Radiolaria, Hertwig leaves the question undecided whether it is the more natural arrangement to make, on the one hand, the Heliozoa, Radiolaria, and Thalamophora three distinct and co-equal equivalent groups, or, on the other hand, to form two great groups—the one containing the Heliozoa and Radiolaria, the other containing the marine and freshwater Thalamophora.

On the whole, I am at present inclined to regard the Radiolaria as an altogether distinct group, and not to unite it with the Heliozoa; and at the same time it seems to me to be unquestionable that of all the above Protozoa, the Heliozoa are those which come nearest to the Radiolaria.

In an earlier paper\* he denied that any near relationship existed between the Heliozoa and Radiolaria. He made this denial on the ground of the supposed cellular nature both of the external and internal alveoli, and also of the "*wasserhellen Bläschen*" as well as on other accounts. As he has now, however, become convinced that alveoli are but vacuoles without membranous walls, and that the "*wasserhellen Bläschen*" are but nuclei, these two reasons fall to the ground. The following distinctions, however, seem still to remain intact:—

- (1) A porous capsular membrane present in the *Radiolaria*, absent in the *Heliozoa*.
- (2) A gelatinous investment present in the *Radiolaria*, absent in the *Heliozoa*.
- (3) Reproduction in the *Radiolaria* by means of numerous zoospores †, each with a nucleus and flagellum, but with

\* See Hertwig and Lesser, "Ueber Rhizopoden und denselben nahestehende Organismen," *Archiv für mikrosk. Anat.* vol. x. Suppl.-Heft, p. 147.

† Such parts have not yet been found in any other Rhizopods, least of all in the Heliozoa, in which a single process of division gives rise to a small number of individuals. The zoospores of Radiolaria are most nearly resembled by those of *Myxomycetes*; but there the reproductive process is very different.

no vacuoles. In the *Heliozoa*, on the other hand, the much fewer separated reproductive parts have each two flagella (as in most Rhizopods), several contractile vacuoles, and a nucleus with vacuoles and nucleoli.

- (4) Yellow cells present in almost all *Radiolaria*, absent in *Heliozoa*.
- (5) The *Radiolaria* are entirely marine, while the yet known *Heliozoa* are almost entirely freshwater.
- (6) The pseudopodia of Radiolarians have no axis-fibre similar to that so often found in the *Heliozoa*.

The similarity between these two groups in external form and chemical composition is undeniable; but, as Hertwig points out, very many of the *Radiolaria* depart widely from the spherical form, while the similarity of chemical composition cannot be considered as a distinction of great weight, seeing that the similarity is shared with many other lowly organisms of quite different affinities. The distinction as to the medium inhabited is also much weakened by the discovery of the salt-water *Heliozoa*, *Pinnacocystis rubicunda* and *Actinolphus pedunculatus*.

Again, though the differences which exist between the reproductive processes (above enumerated as No. 3) are very great, yet we must recollect that there are also great differences in this respect between different *Heliozoa*, while the reproductive processes of so few *Radiolarians* have yet been examined, that it would be rash to feel confident that no important divergencies will be hereafter found to exist amongst them in this respect.

With respect to the capsule itself (which seems to form so very marked a difference) the distinction would be weakened if it should turn out that young *Radiolarians* which have not yet acquired a capsule, nevertheless show a differentiation of their sarcode into an inner and an outer layer, like the medullary and cortical parts of *Heliozoa*; and this may be indicated by Cienkowski\*. The distinction would not only be weakened, but would break down if it should be shown that certain adult Radio-

\* See Archiv für mikrosk. Anat. vol. vii. p. 374, and pl. xxix. fig. 1. He says as to the young condition without a capsule, "Die jungen Kapseln sind nackt ohne Schale in eine strahlende Protoplasmaschicht eingebettet, von keiner scharf conturirten Hülle umgrenzt. In diesem Stadium theilen sie sich häufig durch Abschnürung in zwei Hälften."

larrians have no capsule at all, a condition which seems indicated by Sir C. Wyville Thomson\*.

In spite, however, of these latter considerations, I am inclined, on the strength of the distinctions above enumerated, to keep provisionally apart, as two equivalent and divergent groups, the Heliozoa and the Radiolaria.

As to the unicellular nature of Radiolarians, the most recent researches of Hertwig have convinced him that however diverse may be the contents of the capsule, they are nevertheless only the products of the differentiation of a single cell, such as we find in many small animals and in plants, which are admitted to be unicellular.

The yellow cells, however, stand markedly apart; and if Hertwig is right in his views respecting them, then those true cells must take their rise in a multinucleate sarcode as a true endogenous cell-formation—a rare occurrence.

If, however, the yellow cells should turn out to be parasitic organisms, they will not only thus cease to be mysterious, but the circumstances will render the truly cellular nature of the “centripetal cell-groups” of *Physematium* more improbable, seeing that they will then be the only instance of true cells in the Radiolaria, and thus the existence of some error of observation in this regard will seem more probable.

If Hertwig is right in his view as to the origin of the nuclei of *Thalassicolla*, then we have therein a mode of origin elsewhere unknown amongst animals, viz. nucleoli dividing, passing out from the nucleus, and becoming nuclei themselves. The author’s previous observations † as to nuclei would appear to make his theory less improbable; but it should be duly noted that Professor W. Flemming disputes ‡ Hertwig’s views.

Without venturing to express an opinion in this controversy, I would place on record that Hertwig has come to the conclusion that a multinucleolate cell is potentially multinucleate, as a multinucleate cell is potentially multicellular; and thus we get a

\* His words are:—“In many Radiolarians, and especially in some very peculiar compound forms, a spherical internal chamber, called the ‘central capsule,’ whose function we do not fully understand, is very prominent. This capsule is, however, absent, or at all events exists in a very modified form, in the more typical groups.”—‘Voyage of the Challenger,’ vol. i. p. 232.

† ‘Morphol. Jahrbuch,’ vol. ii. p. 63, pl. iii.

‡ Archiv f. mikrosk. Anat. vol. xiii. 1877, p. 692, pl. xlii.

transition from unicellular to multicellular organisms. Hertwig's view does, in fact, seem to be, as he says it is, the old view, that the nucleolus divides first, and then the nucleus. In support he refers to the labours of Carter, Wallich, Greef, Claparède, and Lachmann, as showing that in the nucleus of Rhizopods numerous nucleoli develop themselves, which pass out from the nucleus and grow in the surrounding protoplasm into Amœbiform bodies with a nucleus and contractile vacuoles. He also refers to Auerbach's multinucleolate nuclei in the tissues of Dipterous larvæ about to assume the pupa condition.

To conclude, the multicellular nature of Radiolarians now depends entirely on the normal nature of their yellow cells, and on the correctness of the observations as to the centripetal cell-groups of *Physematium*.

As has been said, neither of these phenomena can be reposed on as being certainly of the nature of true cells forming part of the normal organization of the Radiolarians in which they have been found; but even if they are so, and if we are compelled therefore to regard Radiolarians as multicellular, their multicellularity is of a radically different kind from that of any of the Metazoa, and none of their parts, whether truly cells or not, have any valid claim to the denomination of a tissue.

#### *Literature.*

In the great work of Professor Haeckel, 'Die Radiolarien,' will be found complete and ample references to all the literature of the Radiolaria antecedent to its publication. Since its appearance the following publications, relating to these animals, have appeared.

EHRENBERG. Abhandlungen der könig. Akad. der Berlin, 1862, pp. 39-74, pls. i.-iii.; 1868, pp. 1-55; 1869, pp. 1-66, pls. i.-iii.; 1870, pp. 1-74, pls. i.-iii.; 1871, pp. 1-150, pls. i. & ii.; 1872, pp. 131-400, pls. i.-xii.; 1875, pp. 1-225, pls. i.-xxx.

(These papers contain notices, with or without figures, on different Radiolarians, with observations on their distribution in time and space.)

ERNST HÆCKEL. Zeitschrift für wissenschaft. Zoologie, vol. xv. p. 342, pl. xxvi., 1865.

(A memoir on the sarcode of Rhizopods, with special references to many Radiolaria, and with descriptions and figures of the new



genus *Actinellius* and the new species *Acanthodesmia polybrocha* and *Cyrtidosphæra echinoides*.)

A. SCHNEIDER. Archiv für Anatomie und Physiologie, p. 509, 1867.

(An histological investigation, showing the comparative unimportance of the extracapsular portion of the sarcode, at least in *Thalassicolla*.)

JAMES DANA. Amer. Journ. of Science and Arts, May 1863, and Ann. & Mag. Nat. Hist. 3rd ser. vol. xii. p. 54, 1863.

(A very short notice of *Sphærozoum*, suggesting a relation between it and sponges.)

WALLICH, Dr. G. C. 'North-Atlantic Sea-bed.' Van Voorst, 1862.

(Unfinished; plates named, but figures unfortunately without descriptions.)

WALLICH, Dr. G. C. On the Structure and Affinities of the *Polycystina*. Quarterly Journal of Microsc. Science, vol. v. (n. s.) 1865, pp. 75-84.

WALLICH, Dr. G. C. Ann. & Mag. Nat. Hist. 4th ser. vol. iii. p. 97, 1869.

(Observations on *Thalassicolla* and *Sphærozoum*; no mention is here made of Haeckel's monograph.)

ERNST HAECKEL. Jenaische Zeitschrift, vol. v. p. 519, pl. xviii. Republished in 'Biologischen Studien,' pt. 1. See also Quarterly Journal of Microscopical Science, (n. s.) vol. xi. p. 63, pl. v.

(Description, with figures, of the curious form *Myxobrachia*, here first made known.)

ALEX. STUART. Neapolitanische Studien. Göttingen Nachr. 1870, No. 6.

(A work of little value, in which the well-known Foraminifer *Globigerina echinoides* is described as a Radiolarian under the name *Coscinosphæra ciliosa*.)

N. WAGNER. Bulletin de l'Acad. de St. Pétersbourg, vol. xvii. p. 140.

(Herein is noticed a new species of *Myxobrachia*, *M. Cienkowskii*.)

MACDONALD, Dr. J. D. Quarterly Journ. of Microscopical Science, (n. s.) vol. ix. p. 147, pl. xi., 1869.

(In which is briefly treated points concerning *Sphærozoum*, *Collosphæra*, and *Thalassicolla nucleata*.)

MACDONALD, Dr. J. D. Ann. & Mag. Nat. Hist. 4th ser. vol. viii. p. 224, 1871.

(A short paper, containing a notice of *Acanthometra* and *Dictyocha*, with a woodcut of *Astromma Yelvertoni*, and observations on modes of growth.)

L. CIENKOWSKI. Archiv f. mikrosk. Anat. vol. vii. p. 371, pl. xxix., 1871.

(A valuable paper, wherein is first accurately described the formation of zoospores, with observations on the reproduction of *Colloosphæra* and *Collozoum*, and notes upon yellow cells. This paper has been translated in the 'Quarterly Journal of Microscopical Science, (n. s.) vol. xi. p. 396, pl. xviii.)

W. DONITZ. Arch. f. Anat. und Phys. p. 71, plate ii., 1871.

(Observations on Radiolaria, in which he treats of *Thalassicolla*, *Collozoum*, and *Sphærozoum*, describing a new species (*S. Sanderi*) of the last-named genus. He appears, though, to have confounded the earlier with the later stages of *Collozoum*, and fallen into other errors of interpretation: see Hertwig, Zur Hist. d. Rad. pp. 9, 10.)

HERTWIG and LESSER. Archiv f. mikrosk. Anat. vol. x. Suppl. p. 147, 1874.

(In this treatise the question of the relationship of the Radiolaria to the Heliozoa is considered; and they are said to have no near relationship.)

FOCKE, G. W. Zeitschrift für wissen. Zoologie, 1868, vol. xviii. p. 345. Translated in 'Quarterly Journal of Microscopical Science,' vol. ix. 1869, pp. 67-75.

(The author considers some Heliozoa discovered by him as true freshwater Radiolaria; but they do not present true Radiolarian characters.)

W. ARCHER. Quarterly Journal Microsc. Science, (New Ser.) vol. ix. p. 250, 1869.

(Freshwater Heliozoa described, with a reference to Focke's paper, asserting the existence of pulsating vacuoles.)

GREEF. Archiv für mikrosk. Anat. vol. v. p. 464, and vol. xi. p. 1, pls. i. & ii.

(In the former paper the author describes Heliozoa, and is inclined to regard the inner body of *Clathrulina* as representing the Binnenblase of the Radiolaria. In the latter place he reconsiders the homology asserted by some (*e. g.* A. Schneider) to exist

between Radiolarian yellow cells and the green cells of the Heliozoon *Acanthocyrtis*, deciding that the question cannot be settled till the genesis of both cells is understood; but that if they are homologues, then the outer wall of *Acanthocyrtis* cannot be the homologue of a central capsule.)

Also Sitzungs b. d. niederrheinischen Gesellsch. Jan. 1871.

And Sitzungs b. d. Gesellschaft f. Natur. zu Marburg, No. 5, 1875.

CARRUTHERS, W. British Assoc. Reports, 1872, p. 126, and Quart. Journ. Microsc. Science, (n. s.) vol. xii. p. 397, 1872.

(On *Traquairia*, a Radiolarian Rhizopod from the Coal-measures.)

GRENACHER. Zeitschr. f. wiss. Zoologie, vol. xix. p. 289.

(The author, à propos of *Acanthocyrtis viridis*, expresses his opinion that the Heliozoa are a less differentiated branch from a root-stem, from which the Radiolaria are a more differentiated branch, bearing to the latter a relation similar to that borne by the freshwater Hydra to the marine Hydroid polyps.)

HERTWIG, Dr. R. Morphol. Jahrbuch, vol. ii. p. 63, pl. iii.

(In this the author puts forward his views as to the formation of nuclei from so-called nucleoli.)

HERTWIG, Dr. R. Zur Histologie der Radiolarien. Leipzig, 1876.

(A most excellent treatise on the structure and reproduction of *Collozoum inerme*, *Thalassicolla nucleata*, and *Thalassolampe margarodes*, with considerations on the relations borne by the Radiolaria to the other Rhizopods, and the bearing of the facts noted on the cell-theory.)

ZITTEL, KARL A. Handbuch der Paläontologie, I. Band, p. 117, 1876.

(The author notices the fossil Radiolaria of the Mesozoic strata.)

ZITTEL, KARL A. Ueber fossile Radiolarien der ob. Kreide. Zeitschrift d. deutschen geol. Ges. (1876), Band xxviii. Heft 1.

FLEMMING, Prof. WALTHER. Archiv f. mikrosk. Anat. vol. xiii. p. 629, pl. xlii., 1877.

(An elaborate paper, wherein the author takes occasion to criticise and oppose Dr. Hertwig's views as to the nucleus and nucleolus, their multiplication and reproduction.)